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Archaeocyathids from the Atdabanian (Lower Cambrian) of the Altay-Sayan Foldbelt, Russia

Dena V. OSADCHAYA & Dmitriy V. KOTEL'NIKOV
All-Russian Geological Institute, Sredniy prospekt 74,
Saint Petersburg 199026 (Russia)

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ABSTRACT
The stratigraphic distribution of irregular archaeocyaths (archaeocyathids) species in the Atdabanian Stage of the Altay-Sayan Foldbelt is established. One assemblage characterizes the Bazaikha Superhorizon and two assemblages are observed in the Kameshki Horizon. These assemblages are consistent independently of the facies type and traceable throughout Batenevskiy Ridge (carbonate facies), Tuva (volcanic-carbonate facies) and Eastern Sayan (siliciclastic-carbonate facies). This observarion confirms the existence of a single Altay-Sayan basin by the middle Atdabanian time. Three new species (*Loculicyathus voznesenskii*, *Mikhnocyathus irregularis*, *Sakhacyathus karpinskii*) are described and the most typical species are revised and redescribed.

KEY WORDS
Archaeocyathida,
Atdabanian,
Altay-Sayan,
correlations.

RÉSUMÉ
Archéocyathes de l'Atdabanien (Cambrien inférieur) du massif plissé d'Altaï-Saïan, Russie. La répartition stratigraphique des archéocyathes irréguliers (archéocyathides) du massif plissé d'Altaï-Saïan est établie pour l'Atdabanien. Un assemblage caractérise le Superhorizon de Bazaikh et deux assemblages sont observés dans l'Horizon de Kameshki. Ces assemblages concordent, indépendamment du type de faciès, et peuvent se suivre à travers la crête de Batenev (faciès carbonaté), la région de Tuva (faciès volcano-carbonaté) et le Saïan oriental (faciès silicoclastique et carbonaté). Cette observation confirme l'existence d'un seul bassin dans l'Altaï-Saïan au milieu de l'Atdabanien. Trois nouvelles espèces sont décrites (*Loculicyathus voznesenskii*, *Mikhnocyathus irregularis*, *Sakhacyathus karpinskii*) ; les autres espèces sont révisées et redécrites.

MOTS CLÉS
Archeocyathida,
Atdabanien,
Altaï-Saïan,
corrélations.

INTRODUCTION

The Altay-Sayan Foldbelt is a mountaineous region of Siberia (SW of the Siberian Platform). It includes Kuznetskiy Alatau, Batenevskiy Ridge, Altay Mountains, Shoriya Mountains, Eastern and Western Sayan and Tuva. Thick and continuous Lower Cambrian strata of the Altay-Sayan Foldbelt are, in addition to those of the Siberian Platform, a key sequence for the Lower Cambrian stage and zone subdivisions that are accepted in Russia; Botomian and Toyonian archaeocyathan zones are established here. However, these zones were entirely based on regular archaeocyaths whose geographic distribution is limited and, as a result, their significance for correlations.

Irregular archaeocyaths (archaeocyathids) of the Altay-Sayan Foldbelt were poorly known. Too many species were commonly and wrongly attributed to the genera "*Dictyocyathus*" and "*Loculicyathus*". Gravestock (1984) initiated new researches into the morphology of irregular archaeocyaths and this was expanded in the major book of Debrenne & Zhuravlev (1992). The work of the latter authors develops a new systematic of irregular archaeocyaths based on morphology, ontogeny and homologous variability; they provide a complete diagnosis, revised systematic affinities and an outline of stratigraphic distribution of all genera. There, we revise the Atdabanian irregular archaeocyath assemblages of the Altay-Sayan Foldbelt in the framework of this new systematics based on abundant material that we collected from Batenevskiy Ridge, Eastern Sayan and Tuva, mainly from the stratotypes of zones of the Bazaikha Superhorizon and Kameshki Horizon. These local subdivisions of the Altay-Sayan Foldbelt correspond to the Atdabanian Stage.

GEOLOGICAL SETTING

Batenevskiy Ridge (Sukhie Solontsy Massif)-Carbonate Section Type

Calcimicrobial and calcimicrobial-archaeocyathan reefal carbonates dominate in the Batenevskiy Ridge. These are massive gray and light gray limestones with unevenly spaced fossils. Irregular archaeocyaths are studied from the Solontsy Biohermal Massif in Sukhie Solontsy Valley, Tolcheya Village area (Fig. 1). The Solontsy Biohermal Massif spreads latitudinally for 8 km as a discontinuous belt of Lower Cambrian reefal limestones from 1000 to 1200 m in thickness. The Atdabanian strata are 600 m in thickness.

The *Nochoroicyathus mariinskii* Zone is at the base of the Bazaikha Horizon in Batenevskiy Ridge. The most complete assemblage of this zone is derived from the reference section of Krutoy Log. Additional data are obtained from sections of 740.6 m, 786 m and 803.5 m altitudes. The *Nochoroicyathus mariinskii* Zone is typified by genera *Cambrocyathellus*, *Neoloculicyathus*, *Dictyocyathus*, *Dictyosycon*, *Tabulacyathellus* and *Dictyofavus*. The most common species are *Cambrocyathellus communis* (Fonin), *C. similiseptus* (Voronin), *C. tuberculatus* (Vologdin), *C. kundatus* (Zhuravleva), *C. minutus* (Vologdin), *Neoloculicyathus primus* Voronin, *Loculicyathus membranivestites* Vologdin, *Dictyocyathus confertus* Fonin, *Archaeopharetra marginata* (Fonin), *Dictyosycon radiatus* (Zhuravleva), *Dictyofavus* sp., *D. lepidus* (Fonin), *D. obtusus* Gravestock, *Tabulacyathellus* sp. and *T. bidjaensis* Missarzhevskiy. Species of *Cambrocyathellus* are especially abundant at this level.

From the base of the following *Gordonicyathus howelli* Zone, the former archaeocyathan assemblage steadily declines. Single representatives of the earlier assemblage only exist at the top of the *Gordonicyathus howelli* Zone. In the lower part of this zone *Cambrocyathellus* sp., *C. communis*, *C. similiseptus*, *C. tuberculatus*, *C. kundatus*, *Neoloculicyathus primus*, *Loculicyathus membranivestites*, *Paranacyathus* ? sp., *Mikhnocyathus irregularis* Kotel'nikov n.sp., *Dictyocyathus confertus*, *Archaeopharetra marginata*, *Dictyosycon* sp., *Dictyofavus lepidus*, *Tabulacyathellus bidjaensis*, and *Kechikacyathus* ? sp. are present. *Cambrocyathellus neiburgianus* (Vologdin) appears in the upper part of the zone and *Loculicyathus membranivestites* becomes the most abundant species there (Fig. 2).

The same species is the only common archaeo-

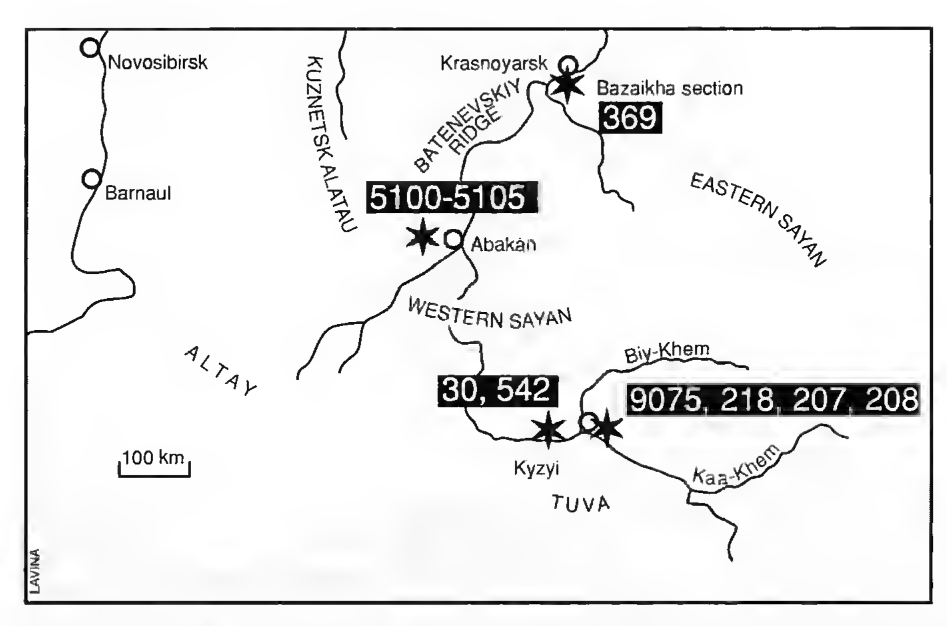


FIG. 1. — Situation of sections (Altay-Sayan Foldbelt, Russia). Localities **5100-5105**: Solontsy Biohermal Massif, Sukhie Solontsy Valley, Krutoy Log section, Batenevskiy Ridge; locality **369**: Bazaikha River section, Batenevskiy Ridge (Eastern Sayan); localities **30, 542**: Bayan Kol River section (Tuva); locality **9075**: Vadi Bala section; locality **218**: Terektyg Khem River section; localities **207, 208**: Tapsa river Basin, Il'chir River section (Central Tuva). Scale: 1/10 000 000.

cyathid of the Kameshki Horizon in the Krutoy Log and other sections of the Solontsy Biohermal Massif. Rare *Cambrocyathellus*, *Neoloculicyathus* and *Dictyocyathus* occur at the base of the horizon.

TUVA VOLCANIC-CARBONATE SECTION TYPE

Bayan Kol River Section

The Bayan Kol River is a left tributary of the Enisey River in Central Tuva. The reference section occurs in the lower course of the Bayan Kol River (Fig. 1). The lower subformation of the Bayan Kol Formation which thickness is 1100 m is of early Atdabanian age. On the left bank of the Bayan Kol River, the subformation includes sandstone-gravelstone-conglomerate unit with restricted red and light gray reefal limestones. Reefal limestones consist of kaliptra, kaliptrate bioherms, biohermal and biostromal beds.

The *Nochoroicyathus mariinskii* Zone of the Bazaikha Superhorizon is restricted to the basal red reefs and is characterized here by *Cambrocyathellus* sp., *C. tuberculatus*, *C. kundatus*, *Sakhacyathus karpinskii* Osadchaya *et* Kotel'nikov n.sp., *Loculicyathus voznesenskii* Osadchaya *et* Kotel'nikov n.sp., *Archaeopharetra marginata*, *Dictyofavus lepidus*, and *Dictyocyathus confertus*. Modular forms of *Cambrocyathellus*, *Archaeopharetra* and *Dictyofavus* are common. *Cambrocyathellus* is the most diverse genus and *Archaeopharetra* dominates volumentrically.

Archaeocyathan assemblage of the *Gordonicyathus howelli* Zone is present in the upper gray reefs of the lower subformation. Only rare representatives of the earlier assemblage, *Cambrocyathellus tuberculatus*, *C. kundatus*, *Sakhacyathus karpinskii*, *Neoloculicyathus* ex gr. *primus*, and *Archaeopharetra marginata* are found. The Kameshki Horizon assemblage is not included in the present study.

Tapsa River Sections

The sections of the Tapsa River basin occur along the Vadi Bala Valley and Bol'shoy Il'chir Creek in the Cherbi Village area of the Taapsa and Kaa-Khem rivers interfluve, Central Tuva. The Il'chir Formation which is up to 2000 m in thickness, represents the Atdabanian Stage here. The lower

part of formation (200-700 m) contains lilac tuff-conglomerates, tuffgravelates, tuffits and tuffsandstones with scarce limestone lenses. The upper carbonate part of formation (700-1300 m) includes dark gray platy dolomitic limestones with marker beds of oolitic limestone, above which a reefal limestone with archaeocyaths occurs.

Vadi Bala Section. Archaeocyathan assemblage of the *Nochoroicyathus mariinskii* Zone, Bazaikha Superhorizon, is restricted to a massive reefal limestone of the Vadi Bala Biohermal Massif and includes *Cambrocyathellus similiseptus*, *C. tuberculatus*, *C. minutus*, *Neoloculicyathus* sp., *Dictyocyathus* sp., *Archaeopharetra marginata*, *Dictyosycon radiatus* and *Dictyofavus lepidus*.

Bol'shoy Il'chir Creek Section. Archaeocyaths of the *Gordonicyathus howelli* Zone, Bazaikha Superhorizon, are found in white and red massive reefal limestone overlaying the basal tuffconglomerate. They are represented by *Cambrocyathellus* sp., *C. minutus*, *C. kundatus*, *Loculicyathus membranivestites*, *L. voznesenskii*, *Mikhnocyathus* ? sp., *Archaeopharetra marginata*, and *Tabulacyathellus* sp., among which *Loculicyathus membranivestites*, *L. voznesenskii* and *Mikhnocyathus* ? sp. appear at this level.

To the top of the Bol'shoy Il'chir Creek Section, along the creek upstream, archaeocyaths of the Kameshki Horizon are collected from limestone debris. These archaeocyaths are, *Cambrocyathel-*

LAVINA Archaeocyaths	Krutoy Log	H. 740.6 m	H. 786 m	H. 803.5 m
Cambrocyathellus communis	■ ●	■	■ ●	●
C. similiseptus	■ ●		■ ●	■
C. tuberculatus	■ ●			
C. kundatus	■ ●	■		
C. minutus			■	
C. neiburgianus			■	
Neoloculicyathus primus	■ ●			●
N. ex gr. *chabakovi*	■ ●			
Loculicyathus membranivestites	■ ●	●		
Mikhnocyathus irregularis n.sp.	●			
Dictyocyathus confertus	■	■ ●		
Archaeopharetra marginata	■ ●			■ ●
Dictyosycon radiatus	■ ●		■	
Dictyosycon sp.			●	●
Dictyofavus lepidus	■ ●		●	■
Dictyofavus obtusus	■			
Dictyofavus sp.			●	●
Kechikacyathus sp.	●			
Tabulacyathellus bidzjaensis	■	■ ●	●	■ ●

Fig. 2. — Distribution of Atdabanian irregular archaeocyath species in the Bazaikha Superhorizon of the Solontsy Biohermal Massif, Batenevskiy Ridge. Square, *Nochoroicyathus mariinskii* Zone; circle, *Gordonicyathus howelli* Zone.

lus sp., *C. minutus*, *Loculicyathus membranivestites*, *L. tolli* Vologdin, *Mikhnocyathus irregularis* and *Dictyocyathus* sp. A similar assemblage occurs along the Terektyg Khem Creek of the Tapsa and Kaa Khem rivers interfluve. This assemblage is distinctive in its abundance of branching *Cambrocyathellus minutus* and *Mikhnocyathus irregularis*.

Archaeocyathid assemblages of Tuva. Thus, the following irregular archaeocyath assemblages of the Atdabanian age are established in Tuva: Fourteen species of eight genera, *Cambrocyathellus, Neoloculicyathus, Loculicyathus, Sakhacyathus, Dictyocyathus, Dictyofavus, Dictyosycon* and *Archaeopharetra* characterize the *Nochoroicyathus mariinskii* Zone of the Bazaikha Super-

STAGE — ATDABANIAN
Horizon — Bazaikha; Kameshki
Zones — *N. mariinskii*; *G. howelli*; *H. cyroflexus*; *A. torosus*
Archaeocyaths
Cambrocyathellus communis
C. tuberculus
C. similiseptus
Archaeopharetra marginata
Dictyocyalhus confertus
Neoloculicyathus primus
Tabulacyathellus bidzhaensis
Dictyofavus lepidus
Dictyosycon radiatus
Cambrocyathellus kundatus
Ardrossacyathus karpinskii
Loculicyathus vosnesenskii
Dictyocyathus smoljaninovae
Loculicyathus membranivestites
Cambrocyathellus minutus
Dictyofavus obtusus
Neoloculicyathus chabakovi
Dictyosycon sp.
Tabulacyathellus sp.
Kechikacyathus n.sp.
Cambrocyathellus neiburgianus
Mikhnocyathus irregularis
Dictyocyathus sp.
Neoloculicyathus sp.
Loculicyathus tolli
Cambrocyathellus sp.
Paranacyathus sp.

FIG. 3. — Distribution of Atdabanian irregular archaeocyath species in the Altay-Sayan Fold Belt.

horizon. This generic and specific association is almost identical to that of the Solontsy Biohermal Massif from the Batenevskiy Ridge. Species of *Cambrocyathellus* are especially diverse, and *Archaeopharetra marginata* dominates in abundance.

Nine species are known from the *Gordonicyathus howelli* Zone of the Bazaikha Superhorizon in Tuva: *Cambrocyathellus* sp., *C. minutus*, *C. tuberculatus*, *C. kundatus*, *Neoloculicyathus* ex gr. *primus*, *Loculicyathus membranivestites*, *L. voznesenskii*, *Archaeopharetra marginata* and *Tabulacyathellus* sp. *Loculicyathus* and *Tabulacyathellus* genera appear at this level for the first time.

Only six species have been found in the Kameshki Horizon: *Cambrocyathellus* sp., *C. minutus*, *Loculicyathus membranivestites*, *L. tolli*, *Mikhnocyathus irregularis* and *Dictyocyathus* sp. The archaeocyathan species and generic diversity decreased at this level in Tuva, as well as in the Batenevskiy Ridge. In some sections of Tuva, *Cambrocyathellus minutus* and *Mikhnocyathus irregularis* become very common.

Eastern Sayan Siliciclastic-Carbonate Type Section

Sections of the Bazaikha River

The Bazaikha River cuts the Cambrian strata in the Northwest of Eastern Sayan on the junction of the Altay-Sayan Foldbelt and the Siberian Platform, in the Torgashino Ridge. The Torgashino Massif which occurs in the Mana Depression has been proposed to be a large reefal massif (Zadorozhnaya 1983). The massif formed during the whole Early Cambrian and the beginning of Middle Cambrian. Atdabanian strata cropped out on the southern slope of the Torgashino Ridge, in the Kaltat River mouth area.

The *Nochoroicyathus mariinskii* Zone of the Bazaikha Superhorizon is restricted to the basal Bazaikha Member which consists of red limey sandstones, gravelites and limestones. Six genera of archaeocyathids are found in the member which include *Cambrocyathellus*, *Neoloculicyathus*, *Loculicyathus*, *Dictyofavus*, *Dictyosycon* and *Sakhacyathus*. The assemblage consists of twelve species which are *Cambrocyathellus* sp., *C. tuberculatus*, *C. neiburgianus*, *C.* ex gr. *similiseptus*, *Neoloculicyathus* sp., *N. primus*, *Sakhacyathus* sp., *Loculicyathus membranivestites*, *Dictyofavus lepidus*, *D. obtusus*, *Dictyosycon* sp. and *D.* ex gr. *radiatus*. There is striking similarity of this assemblage to the coeval ones discussed above. The only difference is an absence of species of *Dictyocyathus* and *Tabulacyathellus*.

The *Gordonicyathus howelli* Zone assemblage is restricted to the upper part of the siliciclastic-carbonate Bazaikha Member and the lower part of massive light gray reefal limestones of the Torgashino Formation. The same irregular archaeocyath association occurs here, namely *Cambrocyathellus* sp., *C. similiseptus*, *C.* ex gr. *kundatus*, *Neoloculicyathus* sp., *N. primus*, *N.* ex gr. *chabakovi* Konyushkov, *Loculicyathus membranivestites*, *Paranacyathus* ? sp., *Archaeopharetra* sp., *Dictyosycon* sp., *D.* ex gr. *radiatus* and *D.* ex gr. *gravis*. *Sakhacyathus*, *Dictyocyathus* and *Mikhnocyathus* appear in the transitional beds to the Kameshki Horizon. Peculiarities of this assemblage consist in a diversity of *Neoloculicyathus* and *Dictyosycon* genera and almost complete absence of *Dictyofavus* which is abundant in the underlying strata.

Conclusions

The possibility to use archaeocyathid assemblages (instead of ajacicyathid ones) for correlation of Early Cambrian strata in the Altay-Sayan Foldbelt is demonstrated here for the first time.

A constancy in the specific and generic composition of Atdabanian archaeocyathid assemblages through the Altay-Sayan Foldbelt is observed in spite of a facies difference between carbonates of the Batenevskiy Ridge, volcano-carbonates of Tuva and siliciclastic-carbonates of Eastern Sayan.

The *Nochoroicyathus mariinskii* Zone assemblage declines steadily through the *Gordonicyathus howelli* Zone strata until an almost complete disappearance at the Bazaikha Superhorizon-Kameshki Horizon boundary. At the Bazaikha Superhorizon-Kameshki Horizon boundary, a notable shift in an archaeocyath composition is indicated. *Loculicyathus* dominates from the base of the Kameshki Horizon.

An identity of archaeocyathid assemblages in the Batenevskiy Ridge, Tuva and Eastern Sayan sug-

gests the existence of single basin during the Atdabanian epoch throughout the whole territory.

SYSTEMATIC PALEONTOLOGY

New and revised species are described in this section. Authors follow the systematics and terminology of irregular archaeocyaths (archaeocyathids) developed by Debrenne & Zhuravlev (1992). The figured type material is housed in the Muséum national d'Histoire naturelle (MNHN), Paris, France; other specimens are in the Central Scientific-Research Geological Exploring Museum (CNIGRm), Saint Petersburg, Russia. Other abbreviations include the Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia (PIN) and the South Australian Museum, Adelaide, South Australia (SAM).
All dimensions are in millimetres.

Phylum PORIFERA Grant, 1872
Class ARCHAEOCYATHA Bornemann, 1884
Order ARCHAEOCYATHIDA Okulitch, 1935
Suborder LOCULICYATHINA Zhuravleva, 1954
Superfamily LOCULICYATHOIDEA Zhuravleva, 1954
Family LOCULICYATHIDAE Zhuravleva, 1954

Genus *Loculicyathus* Vologdin, 1931

Loculicyathus voznesenskii
Osadchaya *et* Kotel'nikov, n.sp.
(Fig. 4)

HOLOTYPE. — MNHN M810055 (Fig. 4); Central Tuva, Bayan Kol River, locality 542-1; Lower Cambrian, Atdabanian Stage, Bazaikha Superhorizon, *Nochoroicyathus mariinskii* Zone.

ETYMOLOGY. — The species is named after the geologist V. D. Voznesenskiy.

OTHER MATERIAL. — Three well-preserved specimens in transverse sections (CNIGRm).

DISTRIBUTION. — Bazaikha Superhorizon, Atdabanian Stage; Central Tuva.

DIAGNOSIS. — Species with funnel-shaped outer wall pores which pierce the wall in two rows per intersept; inner wall simple bearing spines.

DESCRIPTION
Cup diameter is up to 11.5. Outer wall simple, 0.15-0.2 thick, bearing two rows of funnel-shaped pores per intersept (pore diameter = 0.2-0.3, lintel width = 0.2). Intervallum (width = 2.5) contains pseudosepta which are pierced by five to seven pore rows (pore diameter = 0.2-0.3, pseudoseptum thickness = 0.1). Radial coefficient = 3.7, interseptal coefficient = 1:5-1:6. Inner wall simple (thickness = 0.2-0.25), with one pore row per intersept and spines (pore diameter = 0.4). Vesicles in the intervallum and pellis on both walls are common.

DISCUSSION
This new species differs from *Loculicyathus membranivestites* Vologdin by less numerous pore rows per intersept of the outer wall (two against four), by funnel-shaped outer wall pores and by inner wall spines.

Genus *Cambrocyathellus* Zhuravleva, 1960

Cambrocyathellus similiseptus
(Voronin, 1979)
(Fig. 5)

Robustocyathus similiseptus Voronin, 1979: 99, pl. IX, fig. 1-3.
Cambrocyathellus similiseptus (Voronin) – Debrenne & A. Zhuravlev 1992: 122.

HOLOTYPE. — PIN 2404-11; Voronin, 1979, pl. IX, fig. 1; Western Mongolia, Khasagt Khairkhan Ridge; Lower Cambrian, Atdabanian Stage.

OTHER MATERIAL. — Twenty well-preserved specimens (CNIGRm).

DISTRIBUTION. — Bazaikha Superhorizon, Atdabanian Stage; Kuznetskiy Alatau, Batenevskiy Ridge, Tuva, Eastern Sayan, Mongolia.

DESCRIPTION
Cup diameter is up to 5-6. Outer wall simple of



FIG. 4. — *Loculicyathus voznesenskii* Osadchaya *et* Kotel'nikov, n.sp., holotype MNHN M81005, transverse section, *Nochoroicyathus mariinskii* Zone, Bazaikha Superhorizon, Atdabanian Stage; locality 542-1, Bayan Kol River section, Central Tuva, Russia. Scale bar: 1 mm.

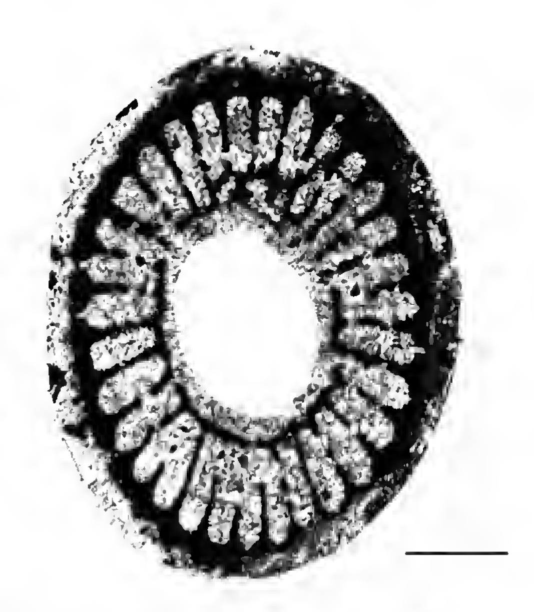


FIG. 5. — *Cambrocyathellus similiseptus* (Voronin), specimen CNIGRm 12917/4, transverse section, *Nochoroicyathus mariinskii* Zone, Bazaikha Superhorizon, Atdabanian Stage; locality 9075-2, Vadi Bala section, Central Tuva, Russia. Scale bar: 1 mm.

Cambrocyathellus-type, 0.1 thick, bearing a single row of rounded pores per intersept (pore diameter = 0.1). Intervallum (width = 1-1.5) is filled with pseudosepta which are pierced by four to five pore rows (pore diameter = 0.1, pseudoseptum thickness = 0.1). Radial coefficient = 7.5, intersept coefficient = 1:4. Inner wall simple, with one pore row per intersept (pore diameter = 0.15, wall thickness = 0.05). Vesicles are present in the intervallum.

DISCUSSION

Cambrocyathellus similiseptus differs from *C. tuberculatus* (Vologdin) by thicker pseudosepta (0.1 against 0.03) and by thinner inner wall (0.05 against 0.1).

Genus *Mikhnocyathus* Maslov 1957

Mikhnocyathus irregularis
Kotel'nikov, n.sp.
(Fig. 6)

HOLOTYPE. — MNHN M81006; Central Tuva, Tapsa River basin, Terektyg Khem River, locality 218; Lower Cambrian, Atdabanian Stage, Kameshki Horizon, *Nalivkinicyathus cyroflexus* Zone.

ETYMOLOGY. — *Irregularis* (Lat.) = irregular.

OTHER MATERIAL. — Fifty well-preserved specimens (CNIGRm).

DISTRIBUTION. — *Gordonicyathus howelli* Zone, Bazaikha Superhorizon-*Nalivkinicyathus cyroflexus* Zone, Kameshki Horizon, Atdabanian Stage; Batenevskiy Ridge, Tuva.

DIAGNOSIS. — Bowl-like cups; outer wall with numerous pore rows per intersept, highly porous pseudosepta and abundant plate tabulae.

DESCRIPTION

Cup diameter above 30. Outer wall simple of *Cambrocyathellus*-type, pierced by four to five rows of rounded pores per intersept (pore diameter = 0.07, lintel width = 0.1, wall thickness = 0.1). Intervallum of 1.5 in width, containing pseudosepta pierced by seven to ten pore rows (pseudoseptum thickness = 0.05, pore diameter 0.05), together with plate tabulae. Interseptal coefficient = 1:2-1:2.5. Tabulae are developed at different levels in adjacent intersepts, a single tabula may be continuous for two to three intersepts. Tabulae are convex, bearing five to six pore rows per intersept (pore diameter = 0.05-0.07,

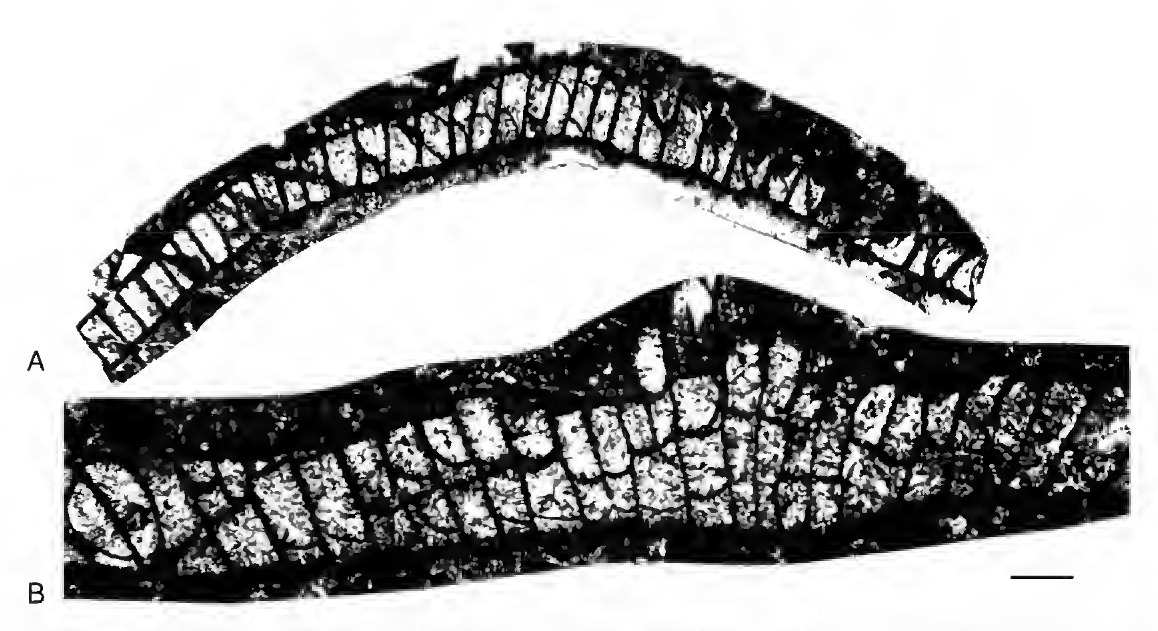


Fig. 6. — *Mikhnocyathus irregularis* Kotel'nikov, n.sp.; **A**, holotype MNHN M81006, fragment of transverse section; **B**, paratype MNHN M81007, fragment of transverse section, *Nalivkinicyathus cyroflexus* Zone, Kameshki Horizon, Atdabanian Stage; locality 218, Terektyg Khem River section, Central Tuva, Russia. Scale bar: 1 mm.

tabula thickness = 0.05). Inner wall simple, with three to four pore rows per intersept (wall thickness = 0.07, pore diameter = 0.05). Vesicles are abundant in the intervallum.

Discussion

This new species differs from *Mikhnocyathus zolaensis* Maslov by more numerous pore rows per intersept of the outer wall (four to five against three) and of pseudosepta (seven to ten against five to six), as well as by more abundant tabulae, few being present since juvenile stages (cup diameter = 3.5-9.5 with interseptal coefficient = 1:1-1:1.5 only).

Superfamily Sakhacyathoidea
Debrenne *et* A. Zhuravlev, 1990
Family Sakhacyathidae
Debrenne *et* A. Zhuravlev, 1990

Genus *Sakhacyathus*
Debrenne *et* A. Zhuravlev, 1990

Sakhacyathus karpinskii
Osadchaya *et* Kotel'nikov, n.sp.
(Fig. 7)

Holotype. — MNHN M81008; Central Tuva, Bayan Kol River, locality 30-1; Lower Cambrian, Atdabanian Stage, Bazaikha Superhorizon.

Etymology. — The species is named after the Academician A. P. Karpinskiy.

Other material. — Five well-preserved specimens in transverse and oblique sections, MNHN M81007, paratypes in CNIGRm.

Distribution. — Bazaikha Superhorizon, Atdabanian Stage; Central Tuva.

Diagnosis. — Species with two outer wall pore rows per intersept.

Description

Modular sheet-like and solitary skeletons with a transverse folding. Outer wall pustular bearing two rows of pores per intersept (wall thickness = 0.15-0.20, pore diameter = 0.15-0.2, lintel width = 0.08-0.1). Intervallum (1-1.5 in width) contains non porous to sparsely porous pseudosepta (pore diameter = 0.1-0.12, thickness = 0.07-0.1). Interseptal coefficient = 1:3. Inner wall simple, 0.1-0.2 thick, with two to three pore rows per intersept (pore diameter = 0.1-0.2). Vesicles are present in the intervallum and a

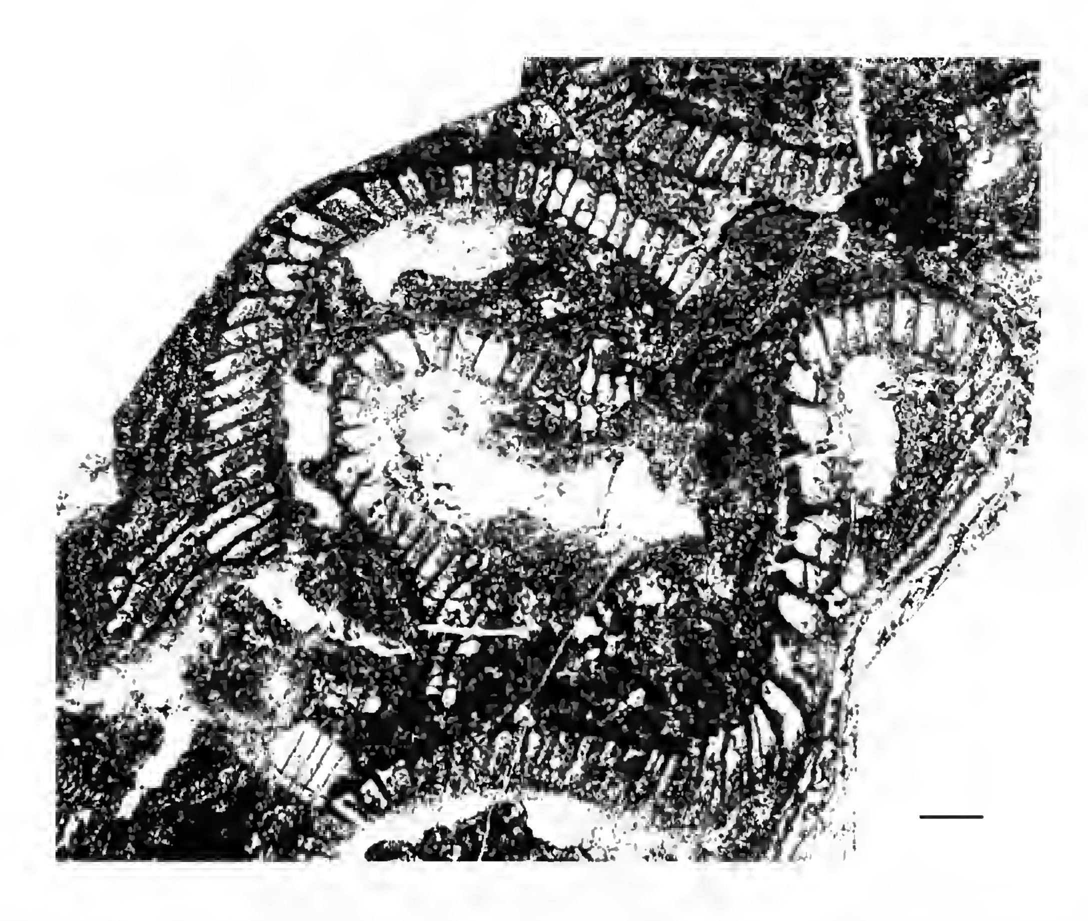


Fig. 7. — *Sakhacyathus karpinskii* Osadchaya *et* Kotel'nikov, n.sp., holotype MNHN M81008, oblique transverse section of a modular form, *Nochoroicyathus mariinskii* Zone, Bazaikha Superhorizon, Atdabanian Stage; locality 30-1, Bayan Kol River section, Central Tuva, Russia. Scale bar: 1 mm.

secondary thickening is developed in the lower part of the cup.

Discussion

This new species differs from *Sakhacyathus subartus* (Zhuravleva) by more numerous pore rows per intersept of the outer wall (two against one).

Suborder ARCHAEOCYATHINA
Okulitch, 1935
Superfamily Dictyocyathoidea
Taylor, 1910
Family Dictyocyathidae
Taylor, 1910

Genus *Dictyocyathus* Bornemann, 1891

Dictyocyathus confertus Fonin, 1982
in Voronin *et al.* 1982
(Fig. 8)

Dictyocyathus confertus Fonin – Voronin *et al.* 1982: 94, pl. XXIII, fig. 7.

Holotype. — PIN 3302/360; Voronin *et al.* 1982, pl. XXIII, fig. 7; Western Mongolia, Khasagt Khairkhan Ridge, Salaany Gol River, locality N-226/290; Lower Cambrian, Atdabanian Stage, *Alataucyathus jaroschevitschi*-, *Tabulacyathellus bidzhaensis*-, *Pretiosocyathus subtilis* beds.

Other material. — Ten well-preserved specimens (CNIGRm).

Distribution. — Bazaikha Superhorizon-Kameshki Horizon, Atdabanian Stage; Batenevskiy Ridge, Tuva, Eastern Sayan, Mongolia.



FIG. 8. — *Dictyocyathus confertus* Fonin, specimen CNIGRm 12917/5, oblique transverse section, *Nochoroicyathus mariinskii* Zone, Bazaikha Superhorizon, Atdabanian Stage; locality 5101-3, Sukhie Solontsy Valley, Batenevskiy Ridge, Russia. Scale bar: 1 mm.

DESCRIPTION

Cup diameter is up to 7.3. Outer wall basic simple, 0.7 thick, bearing a single pore row per intersept (pore diameter = 0.12-0.15, lintel width = 0.5). Intervallum of 1.5 in width is filled with a dictyonal network. Taeniae are pierced by nine to ten vertical pore rows (pore diameter = 0.15-0.25, thickness of intervalar elements including taeniae and synapticulae = 0.03). Synapticulae are regularly arranged in six to eight rows per intervallum width. Radial coefficient = 12-13, interseptal coefficient = 1:10. Inner wall simple, with one pore row per intersept (pore diameter = 0.1).

DISCUSSION

Dictyocyathus confertus differs from other species of *Dictyocyathus* by thinner skeletal elements and by higher radial coefficient.

Superfamily ARCHAEOCYATHOIDEA
Hinde, 1889
Family ARCHAEOCYATHIDAE Hinde, 1889

Genus *Archaeopharetra*
R. Bedford *et* W. R. Bedford, 1936

Archaeopharetra marginata
(Fonin, 1982) *in* Voronin *et al.* 1982
(Fig. 9)

Salanycyathus marginatus Fonin – Voronin *et al.* 1982: 96, pl. XXIV, figs 1-3.
Salanycyathus ordinatus Fonin – Voronin *et al.* 1982: 97, pl. XXV, figs 1-3.
Salanycyathus disertus Fonin – Voronin *et al.* 1982: 98, pl. XXV, fig. 4.
Flindersicyathus gracilis Fonin – Voronin *et al.* 1982: 109, pl. XXXIII, figs 1-5.
Archaeopharetra marginata (Fonin) – Debrenne & A. Zhuravlev 1992: 121.

HOLOTYPE. — PIN 3302/368; Voronin *et al.* 1982, pl. XXIV, fig. 1; Western Mongolia, Khasagt Khairkhan Ridge, Salaany Gol River, locality N-224/180; Lower Cambrian, Atdabanian Stage, *Alataucyathus jaroschevitschi-*, *Tabulacyathellus bidzhaensis-*, *Pretiosocyathus subtilis* beds.

OTHER MATERIAL. — Ten well-preserved specimens CNIGRm.

DISTRIBUTION. — Bazaikha Superhorizon-Kameshki Horizon, Atdabanian Stage; Kuznetskiy Alatau, Batenevskiy Ridge, Central Tuva, Eastern Sayan, Mongolia.

DESCRIPTION

Cup diameter is up to 18. Outer wall centripetal, 0.1 thick. Two to three pore rows cross an intervalar cell which is formed by pseudotaenial lintels and synapticulae (pore diameter = 0.05-0.1). Intervallum of 1.5-2 in width bearing occasional segmented tabulae and porous pseudotaeniae pierced by five to six vertical pore rows (pore diameter = 0.25-0.35). Synapticulae are irregularly spaced in two to three elements per intervallum width. Radial coefficient = 12-14, interseptal coefficient = 1:4-1:5. Inner wall simple, with one pore row per intersept and spines (thickness = 0.05, pore diameter = 0.1-0.2).

DISCUSSION

Archaeopharetra marginata differs from *A. itma-*

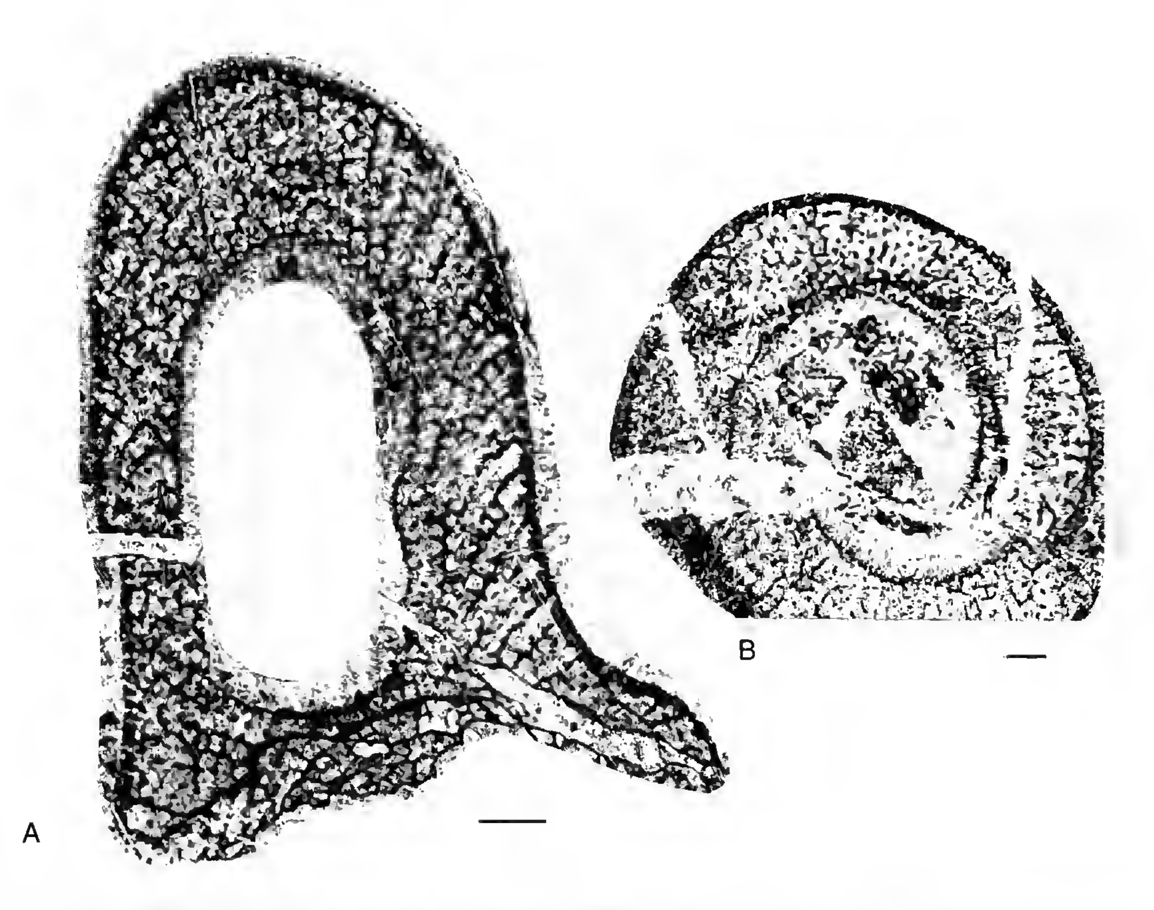


FIG. 9. — *Archaeopharetra marginata* (Fonin), **A**, specimen CNIGRm 12917/8, oblique longitudinal section, locality 9075-1, Vadi Bala section, Central Tuva; **B**, specimen CNIGRm 12917/9, transverse section, locality 5101-8, Sukhie Solontsy Valley, Batenevskiy Ridge; *Nochoroicyathus mariinskii* Zone, Bazaikha Superhorizon, Atdabanian Stage; Russia. Scale bars: 1 mm.

tiensis (Belyaeva) by higher radial coefficient (twelve to fourteen against six to seven) and by smaller diameter of outer wall pores; from *A. yarbili* (Rodionova) by thicker outer wall (0.1 against 0.04) and by less numerous synapticulae.

Suborder DICTYOFAVINA Debrenne, 1991
Superfamily DICTYOFAVOIDEA
Debrenne *et* A. Zhuravlev, 1992
Family DICTYOFAVIDAE
Debrenne *et* A. Zhuravlev, 1992

Genus *Dictyofavus* Gravestock, 1984

Dictyofavus lepidus (Fonin, 1982)
in Voronin *et al.* 1982
(Fig. 10)

Dictyocyathus lepidus Fonin – Voronin *et al.* 1982: 93, pl. XXIII, figs 5-6.

Chouberticyathus lepidus (Fonin) – Debrenne & A. Zhuravlev 1992: 123.

Dictyofavus sp. – Debrenne & A. Zhuravlev 1992, pl. XXVIII, fig. 2.

HOLOTYPE. — PIN 3302/358; Voronin *et al.* 1982, pl. XXIII, fig. 5; Western Mongolia, Khasagt Khairkhan Ridge, Salaany Gol River, locality F-13; Lower Cambrian, Atdabanian Stage, *Alataucyathus jaroschevitschi-*, *Tabulacyathellus bidzhaensis-*, *Pretiosocyathus subtilis* beds.

OTHER MATERIAL. — Twenty well-preserved specimens (CNIGRm).

DISTRIBUTION. — Bazaikha Superhorizon-Kameshki Horizon, Atdabanian Stage; Batenevskiy Ridge, Central Tuva, Eastern Sayan, Mongolia.

Description

Modular massive or solitary skeletons. Diameter of solitary cups is 5-7. Outer and inner walls rudimentary, with cell openings 0.4-0.7 in size. Intervallum is filled with calicles hexagonal in a cross section. Calicles are from 0.5-0.6 to 2.0-2.5 wide, thickness of a calicle wall is 0.1. Calicles bear one, rarely two pore rows per facet. Pore diameter 0.2-0.5. One of the osculi is commonly larger than the others. Vesicles are abundant through the whole cup.

Discussion

Dictyofavus lepidus differs from other species of *Dictyofavus* by thicker intervalar elements and by differenciation of osculi.

Dictyofavus obtusus Gravestock, 1984 (Fig. 11)

Dictyofavus obtusus Gravestock, 1984: 98, fig. 50C-F. – Zhuravlev & Gravestock 1994: 46, fig. 6B (synonymy).

Holotype. — SAM P21666 is not figured. A paratype SAM P21668 which is figured by Gravestock, 1984, fig. 50D-E, is chosen here as the lectotype; South Australia, Wilkawillina Gorge, section I; Lower Cambrian, Atdabanian Stage, *Warriootacyathus wilkawillinensis* Zone.

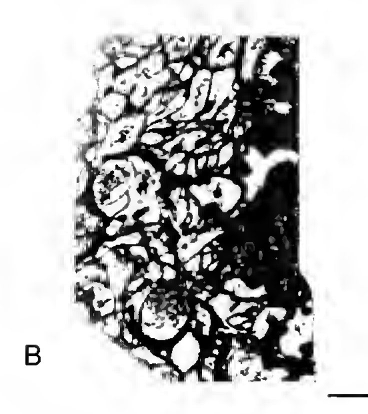
Other material. — Fifteen well-preserved specimens (CNIGRm).

Distribution. — Bazaikha Superhorizon, Atdabanian Stage; Batenevskiy Ridge, Central Tuva, Eastern Sayan and *Warriootacyathus wilkawillinensis-Spirillicyathus tenuis* Zones, Atdabanian Stage, Flinders Ranges and Yorke Peninsula, South Australia.

Description

Modular massive skeletons commonly consisting of two to three individuals. Diameter of a single individual is up to 6, 2-3.5 apart from each other. Outer and inner walls are rudimentary, with cell openings 0.2-0.3 in size. Intervallum is filled with calicles hexagonal in a cross section. Calicles are up to 0.3-0.4 wide, thickness of a calicle wall is 0.05. Calicles bear one pore row per facet (pore diameter = 0.01-0.04). In places, pellis is present on the outer wall.





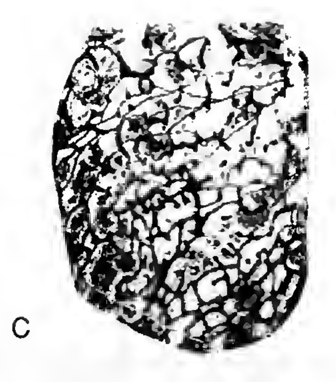


Fig. 10. — *Dictyofavus lepidus* (Fonin). **A**, specimen CNIGRm 12917/10, transverse section, locality 369, Bazaikha River section, Eastern Sayan; **B**, specimen 12917/11, fragment of transverse section, Central Tuva; **C**, specimen CNIGRm 12917/12, fragment of transverse section; locality 5101-7, Sukhie Solontsy Valley, Batenevskiy Ridge; *Nochoroicyathus mariinskii* Zone, Bazaikha Superhorizon, Atdabanian Stage; Russia. Scale bars: 2 mm.

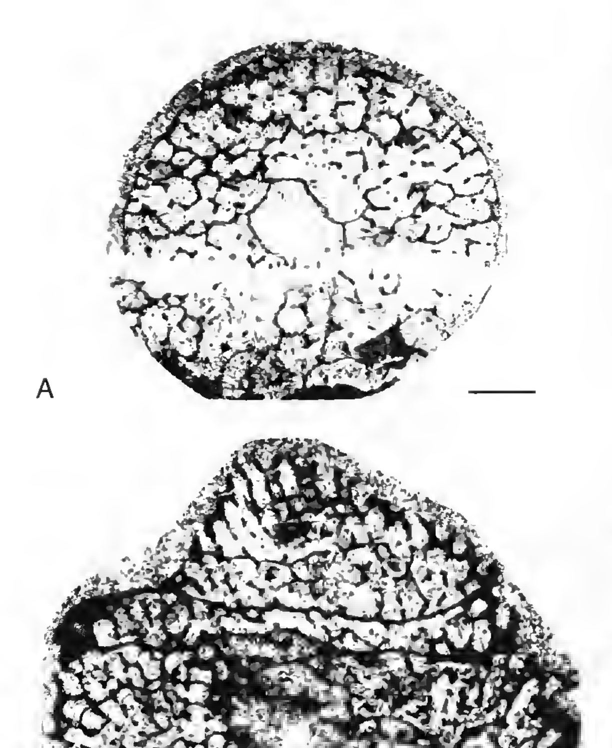


FIG. 11. — *Dictyofavus obtusus* Gravestock, **A**, specimen CNIGRm 12917/6, transverse section, locality 1808, Bazaikha River section, Eastern Sayan; **B**, specimen CNIGRm 12917/7, oblique longitudinal section, locality 5100-9, Sukhie Solontsy Valley, Batenevskiy Ridge; *Nochoroicyathus mariinskii* Zone, Bazaikha Superhorizon, Atdabanian Stage; Russia. Scale bars: 1 mm.

DISCUSSION

Dictyofavus obtusus differs from *D. lepidus* (Fonin) by smaller calicles and by thinner calicular wall.

Acknowledgements

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Mayulestes ferox, a borhyaenoid (Metatheria, Mammalia) from the early Palaeocene of Bolivia. Phylogenetic and palaeobiologic implications

Christian de MUIZON
URA 12 du CNRS, Laboratoire de Paléontologie, Muséum national d'Histoire naturelle,
8 rue de Buffon, F-75231 Paris cedex 05 (France)

Muizon C. de 1998. — *Mayulestes ferox*, a borhyaenoid (Metatheria, Mammalia) from the early Palaeocene of Bolivia. Phylogenetic and palaeobiologic implications. *Geodiversitas* 20 (1) : 19-142.

ABSTRACT
Mayulestes ferox is a borhyaenoid marsupial from the early Palaeocene of Tiupampa (Bolivia). The holotype and only known specimen is a partial skeleton which is described and discussed below. *Mayulestes ferox* is a member of the family Mayulestidae, a taxon which also includes the species *Allqokirus australis* from the same locality and age, but which is only known by a few isolated molars. *Mayulestes* and *Allqokirus* are the two oldest known borhyaenoids. *Mayulestes* differs from *Allqokirus* in the morphology and proportions of its molars. A major feature of the molars of both genera is the reduction of the entoconid which is regarded here as a synapomorphy of the Mayulestidae. *Mayulestes* has the plesiomorphic marsupial dental formula (I5/i4; C1/c1; P3/p3; M4/m4) and its molar morphology approaches the plesiomorphic marsupial cheek tooth pattern. *Mayulestes ferox* does not have a tympanic process of the alisphenoid, a structure whose presence is generally regarded as a marsupial synapomorphy. Comparison with other borhyaenoid taxa indicates that the lack of tympanic process of the alisphenoid is in fact a plesiomorphic character state for the superfamily, and it is suggested that this feature appeared several times during marsupial evolution. The ear region of *Mayulestes* bears a conspicuous medial process of the squamosal and there is a shallow cavity (the roof of the alisphenoid sinus) between the foramen ovale and the glenoid cavity, excavated within the squamosal anteriorly, the periotic posteriorly, and the alisphenoid between. The contribution of the squamosal to the roof of the alisphenoid sinus is regarded as the key synapomorphy of the borhyaenoids. Other borhyaenoid synapomorphies are: the loss of the prootic canal, the reduction and the loss of the anterolateral process of the maxilla, and the probable loss of epipubic bones. The postcranial skeleton of *Mayulestes* is represented by twenty complete or partial vertebrae, a few ribs and most major limb bones. A comparison with living didelphids, *Pucadelphys*, other borhyaenoids, and several arboreal (or probably arboreal) mammals such as sciurids, tupaiids, procyonids, multituberculates morganucodontids, triconodontids, and *Henkelotherium* reveals that many features of the postcranial skeleton of *Mayulestes* are indicative of

arboreality. These traits are: probable prehensility of the tail; posterodorsally extended posterodorsal angle of the scapula; anteriorly and distally projected acromion; low tubercles of the humerus; circular shape of the head of the humerus; large size of the epicondyloid ridge and distomedially protruding medial epicondyle of the humerus; deep flexor fossa on the medial side of the olecranon of the ulna; morphology of the McV; great mobility of the hip attested by the shallowness of the acetabulum and the strong development of the femoral trochanters; sigmoid shape of the tibia and morphology of its distal articulation; shape and orientation of the ectal facet of the calcaneum; large size of the peroneal process; transversely compressed tuber calcanei. Several other features (size of the neural spine and transverse process of the lumbar vertebrae; morphology of the zygapophyses of the last thoracics and lumbar vertebrae; long, anteriorly bent olecranon of the ulna; eversion of the iliac wing; relative depth of the femoral trochlea; flattened distal epiphysis of the tibia; great length of the tuber calcanei) indicate that *Mayulestes* was a relatively agile, scansorial animal capable of bounding. *Mayulestes* is regarded as a partially arboreal predaceous mammal capable of bounding and of some relatively fast but short runs. *Mayulestes* was certainly fairly agile and could have had an ecological niche close to that of weasels or martens, although more arboreal than the former. Several arboreal features of *Mayulestes* are also found in *Pucadelphys*, a didelphid marsupial from the same locality. Consequently, this genus is also regarded as partially arboreal, although to a lesser extent than *Mayulestes*. The fact that the two oldest skeletons of American marsupials denote arboreal habits reinforces the hypothesis that arboreality is probably a symplesiomorphy within marsupials.

KEY WORDS
Marsupialia,
Borhyaenoidea,
Palaeocene,
Bolivia,
phylogeny,
functional anatomy.

RÉSUMÉ

Mayulestes ferox, *un Borhyaenoidea (Metatheria, Mammalia) du Paléocène inférieur de Bolivie. Implications phylogénétiques et paléobiologiques. Mayulestes ferox* est un marsupial Borhyaenoidea du Paléocène inférieur de Tiupampa (Bolivie). L'holotype et unique spécimen connu est un squelette partiel comprenant le crâne complet, la mandibule incomplète et la plupart des os des membres, lesquels sont décrits et discutés ci-dessous. *Mayulestes ferox* est un représentant de la famille des Mayulestidae, un taxon qui inclut également l'espèce *Allqokirus australis*, provenant de la même localité et du même âge, mais connue uniquement par quelques molaires isolées. *Mayulestes* et *Allqokirus* sont les deux plus anciens Borhyaenoidea connus. *Mayulestes* diffère d'*Allqokirus* par la morphologie et les proportions de ses molaires. Un caractère important des molaires des deux genres est la réduction de l'entoconide qui est considérée ici comme une synapomorphie des Mayulestidae. *Mayulestes* possède la formule dentaire plésiomorphe pour les marsupiaux (I5/i4 ; C/c ; P3/p3 ; M4/m4) et la morphologie de ses molaires est proche du patron plésiomorphe des dents jugales de marsupiaux. *Mayulestes ferox* ne présente pas de processus tympanique de l'alisphénoïde, une structure dont la présence est généralement considérée comme une synapomorphie de marsupiaux. Des comparaisons avec les autres taxons de borhyénoïdes indiquent que l'absence de processus tympanique de l'alisphénoïde est en fait une plésiomorphie pour la superfamille, et il est émis l'hypothèse que ce caractère est apparu plusieurs fois au cours de l'évolution des marsupiaux. Le squamosal de *Mayulestes* présente un processus médial bien développé. Dans la région

auditive, entre le foramen ovale et la cavité glénoïde du squamosal, on observe une cavité peu profonde (le toit du sinus alisphénoïde), creusée dans le processus médial du squamosal antérieurement, dans le périotique postérieurement et dans l'alisphénoïde entre les deux. La participation du squamosal à la constitution du toit du sinus alisphénoïde est considérée ici comme la principale synapomorphie des Borhyaenoidea. Les autres synapomorphies de la superfamille sont la perte du canal prootique, la réduction et la perte du processus antérolatéral du maxillaire et la perte probable des os épipubiens. Le squelette post-crânien de *Mayulestes* est connu par une vingtaine de vertèbres complètes ou partielles, quelques côtes, et par la plupart des principaux os des membres. Une comparaison avec les didelphidés actuels, *Pucadelphys*, les autres Borhyaenoidea et plusieurs mammifères arboricoles (ou supposés arboricoles) tels que les sciuridés, les tupaidés, les procyonidés, certains multituberculés, morganucodontes, triconodontes et *Henkelotherium* révèle que beaucoup de caractères du squelette post-crânien de *Mayulestes* indiquent un mode de vie arboricole (queue probablement préhensile ; angle postéro-dorsal de la scapula étiré postéro-dorsalement ; acromion projeté antérieurement et distalement ; tubercules de l'humérus relativement bas ; forme circulaire de la tête de l'humérus ; grande taille de la crête épiconylienne et projection disto-médiale de l'épicondyle ; profonde fosse des fléchisseurs sur la face médiale de l'olécrâne de l'ulna ; morphologie du McV ; grande mobilité de la hanche attestée par la faible profondeur de l'acétabulum et le développement des trochanters fémoraux ; forme sigmoïde du tibia et morphologie de son articulation distale ; forme et orientation de la facette ectale du calcanéum ; grande taille du processus péronéen et tuber calcanei comprimé transversalement). Plusieurs autres caractères (taille de l'épine neurale et des apophyses transverses des vertèbres lombaires ; morphologie des zygapophyses des dernières vertèbres dorsales et des lombaires ; olécrâne de l'ulna, long et recourbé antérieurement ; éversion de l'aile de l'ilium ; profondeur relative de la trochlée fémorale ; épiphyse distale du tibia aplatie antéro-postérieurement et grande longueur du tuber calcanei) indiquent que *Mayulestes* était un animal relativement agile, capable d'adopter une démarche rapide et de bondir. *Mayulestes* est interprété comme un prédateur partiellement arboricole capable de bonds et de course rapide mais de courte durée. *Mayulestes* était certainement assez agile et a pu avoir une niche écologique voisine de celle des martres et des belettes actuelles. Plusieurs caractères arboricoles de *Mayulestes* sont aussi présents chez *Pucadelphys*, un marsupial didelphidé provenant du même gisement. En conséquence, cette forme est également interprétée comme étant partiellement arboricole, bien qu'à un degré moins poussé que chez *Mayulestes*. Le fait que les deux squelettes les plus anciens de marsupiaux américains possèdent des caractères liés à l'arboricolie renforce l'hypothèse selon laquelle ce mode de vie est probablement une symplésiomorphie chez les marsupiaux.

MOTS CLÉS
Marsupialia,
Borhyaenoidea,
Paléocène,
Bolivie,
phylogénie,
anatomie fonctionnelle.

INTRODUCTION

Borhyaenoids are highly carnivorous South American marsupials which are known from the early Palaeocene to the late Pliocene. The remains are generally isolated teeth and jaws but, although uncommon, some complete or partial skeletons are known. The major collection is that described by Sinclair (1906) which consists of several partial skulls and skeletons obtained from the Santa Cruz beds (middle Miocene) of Patagonia. The specimens are placed in four taxa: *Borhyaena tuberata*, *Prothylacynus patagonicus*, *Cladosictis patagonicus*, and *Sipalocyon gracilis*. Several other skulls of *Prothylacynus* and *Cladosictis* from the Santa Cruz beds are known and have been figured (although not described) by Marshall (1979a, 1981). In Columbia, the "Monkey unit" (late Miocene) of the Honda Group from the upper Magdalena Basin has yielded a complete skeleton of *Lycopsis longirostris* (Marshall 1977a). In Catamarca Province (Departamento de Belén), the Monthermosean beds of the Corral Quemado Formation have produced two partial skeletons of *Thylacosmilus atrox* (Riggs 1934). No skeletons are known from the Palaeogene and the only skulls are those from the Deseadan (late Oligocene-early Miocene) beds of Salla-Luribay (Bolivia) referred to *Sallacyon hoffstetteri* and *Paraborhyaena boliviana* (Petter & Hoffstetter 1983) and an undescribed basicranium referred to *Notogale* under study by the author. Borhyaenoids from the Early Tertiary are rare and no complete skulls and/or partial skeletons have been found in the Palaeogene. This state of things drastically enhances the importance of the discovery of a partial skeleton of borhyaenoid (*Mayulestes ferox*) from the early Palaeocene of the Santa Lucía Formation at Tiupampa (Muizon 1994), which is one of the two oldest known borhyaenoids and probably one of the most complete specimens known in the whole superfamily. The other oldest borhyaenoid is *Allqokirus australis* from the same locality and age as *Mayulestes*, but known by a few teeth only. There are more than 40 Ma between *Mayulestes ferox* and the Santa Cruz bothyaenoids skeletons, more than between the Santacruzian and the last borhyaenoids (approx. 15 Ma).

In a more general context, skull and skeletons of fossil marsupials in the Early Tertiary are extremely rare and the only other marsupial skeleton known from the Palaeocene is that of *Pucadelphys andinus* from the same locality (Marshall & Muizon 1995; Marshall & Sigogneau-Russell 1995). *Asiatherium reshetovi* from the Late Cretaceous of Mongolia (Trofimov & Szalay 1994; Szalay & Trofimov 1996) is the only Mesozoic metatherian known by a fairly complete skeleton. This form is regarded here as a true metatherian, although its very specialised teeth may lead some authors to question its membership in Metatheria. These facts, therefore, raise the importance of *Mayulestes* at the level of Metatheria and, considering the scarcity of early Palaeocene and Late Cretaceous mammals, the discovery of the skeleton of *Mayulestes ferox* represents a major event in the knowledge of early mammals.

The description and interpretation of the skull and the postcranial skeleton of *Mayulestes ferox* are presented below. As is generally the case, it is the skull that provides most of the information on the phylogeny of borhyaenoids and marsupials while the postcranial skeleton is more informative on the locomotion and habitat of *Mayulestes*, although the latter also bears some interesting data on mammal evolution.

Abbreviations

AMNH	American Museum of Natural History, New York, USA;
DGM	Divisão de Geologia e Mineralogia do Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil;
FMNH	Field Museum of Natural History, Chicago, USA;
MHNC	Museo de Historia Natural de Cochabamba, Cochabamba, Bolivia;
MNHN	Muséum national d'Histoire naturelle, Paris, France;
MLP	Museo de La Plata, La Plata, Argentina;
YPFB Pal	Paleontology collections of Yacimientos Petrolíferos fiscales de Bolivia, Santa Cruz, Bolivia;
YPMPU	Yale Peabody Museum, New Haven (ex-collections of the Princeton University), USA;
USNM	United States National Museum of Natural History, Washington D. C., USA.

SYSTEMATIC PALEONTOLOGY

Legion TRIBOSPHENIDA McKenna, 1975
Infraclass METATHERIA Huxley, 1880
Suborder DIDELPHIMORPHIA (Gill, 1872)
Infraorder SPARASSODONTA
Ameghino, 1894

Superfamily BORHYAENOIDEA Ameghino, 1894

DIAGNOSIS. — Carnivorous marsupials with a middle ear epitympanic sinus located anterolateral to the promontorium and formed by the alisphenoid anteriorly (and sometimes ventrally), the petrosal posteriorly, and the squamosal laterally. The Borhyaenoidea are the only known metatherians where the squamosal participates in the composition of the alisphenoid sinus and this feature represents the key synapomorphy of the Borhyaenoidea. Furthermore, the superfamily is also diagnosed by the reduction and the loss of the anterolateral process of the maxilla which form the lateral wall of the fossa for the lower canine on the skull, the loss of the prootic canal (a character state found in some other lineages of marsupials), and, possibly, the loss of the epipubic bones (only probable in four genera, *Mayulestes*, *Cladosictis*, *Prothylacynus* and *Lycopsis*, a feature unknown in other taxa).

NOTA. — Borhyaenoids also present the hypercarnivorous dental functional complex related to the postvallum-prevallid shear (reduction and loss of metaconid and entoconid, increase in size of paraconid, reduction of talonid, reduction of protocone, paracone and stylar shelf, increase in size of metacone and metastylar crest). However, as shown by Archer (1982), Fox (1995) and Muizon & Lange-Badré (1997), this functional complex is a highly homoplastic feature which appears independently in several group of mammals and within these groups. Therefore, if it is true that this synapomorphy diagnoses the Borhyaenoidea, it has a low phylogenetic value and certainly cannot represent a key synapomorphy of the Borhyaenoidea.

Family MAYULESTIDAE Muizon, 1994

DIAGNOSIS. — Borhyaenoidea diagnosed by an important reducrion of the entoconid and the resulting lingual opening of the talonid basin.

TYPE GENUS. — *Mayulestes* Muizon, 1994.

INCLUDED GENERA. — *Mayulestes* Muizon, 1994; *Allqokirus* Marshall *et* Muizon, 1988.

Genus *Mayulestes* Muizon, 1994

TYPE SPECIES. — *Mayulestes ferox* Muizon, 1994.

DIAGNOSIS. — The same as the only species referred to *Mayulestes*.

Mayulestes ferox Muizon, 1994

DIAGNOSIS. — *Mayulestes ferox* differs from *Allqokirus australis* in the smaller L/W ratio of its upper molars, in the greater depth of the ectoflexus, in the larger stylar cusp D with a low lingual crest which runs towards the lingual extremity of the metacrista, in the metacrista which does not overhang the base of the crown posteriorly, in the straight posterior edge of the upper molars, in the more robust and longer protocone, and in its narrower and more slender lower molars.

NOTA. — Since the only other species of the family (*Allqokirus australis*) is known by upper and lower molars only, the diagnosis of *Mayulestes ferox* refers to molar morphology only.

HOLOTYPE. — MHNC 1249, a partial skeleton with almost complete skull; right hemimandible lacking the vertical ramus, p2 and p3; left hemimandible lacking the vertical ramus, portion of the horizontal ramus anterior to the posterior root of p2, and the trigonid of m3; atlas lacking the ventral arch; axis; centrum of the ?third cervical vertebra; ?fifth cervical vertebra lacking the neural arch; centra of two anterior thoracic vertebrae; one complete anterior thoracic vertebra; two last thoracic vertebrae; five first lumbar vertebrae with L4 lacking most of the neural arch; two anterior caudal vertebrae; two posterior caudal vertebrae; two anterior ribs; two median ribs; right scapula, almost complete; both humeri; complete left ulna; proximal extremity of the right ulna; left radius; right unciform; left McIII and V; left innominate lacking the anteroventral part of the pubis; part of the right innominate (acetabulum and posterior portion of the ilium); left femur lacking part of the diaphysis and the medial distal condyle; right femur lacking part of the greater trochanter and part of the diaphysis; right tibia; distal extremity of the right fibula; right calcaneum; distal extremity of the left calcaneum; left MtIII and IV.

HYPODIGM. — Type specimen only.

LOCALITY, HORIZON AND AGE. — The specimen was collected on the site 1 ("the quarry"), at the locality of Tiupampa, situated about 95 km southeast of Cochabamba (Mizque Province, Department of Cochabamba, Bolivia). Site 1 (see Gayet *et al.* 1992; Muizon & Marshall 1992; Marshall *et al.* 1995 for

locality map) at Tiupampa has yielded an abundant vertebrate fauna of the Santa Lucía Formation.
The vertebrate fauna includes: Osteichthyes (Dipnoi, Telesotei), Amphibia (Anura, Gymnophiona), Reptilia [Chelonia, Squamata (Lacertilia and Ophidia), Crocodilia], and Mammalia.
An updated list of the mammal fauna is given below. Suprafamilial classification of marsupials follows Szalay (1994) and Sparassodonta are regarded as an infraorder of the suborder Didelphimorphia, following Muizon *et al.* (1997). The other Didelphimorphia are included in the new infraorder Didelphodonta:

Class MAMMALIA

Infra-class METATHERIA
Order DIDELPHIDA
Suborder ARCHIMETATHERIA
Family PERADECTIDAE
Peradectes cf. *austrinum*
Suborder SUDAMERIDELPHIA
Family CAROLOAMEGHINIIDAE
Roberthoffstetteria nationalgeographica
Suborder DIDELPHIMORPHIA
Infraorder DIDELPHODONTA new
Family PUCADELPHYDAE new
Pucadelphys andinus
? *Andinodelphys cochabambensis*
Family ? DIDELPHIDAE
Incadelphys antiquus
Mizquedelphys pilpinensis
Tiulordia floresi
Family JASKHADELPHYDAE
Jaskhadelphys minutus
Infraorder SPARASSODONTA
Family MAYULESTIDAE
Mayulestes ferox
Allqokirus australis
Order GONDWANADELPHIA
Suborder MICROBIOTHERIA
Family MICROBIOTHERIIDAE
Khasia cordillierensis

Infra-class EUTHERIA
Order LEPTICTIDA
Family PALAEORYCTIDAE ?
Cf. *Cimolestes* sp.
Family indet.
Gen. and sp. indet.
Order PANTODONTA
Family ALCIDEDORBIGNYIDAE
Alcidedorbignya inopinata
Order CONDYLARTHRA
Family MIOCLAENIDAE
Molinodus suarezi
Tiuclaenus minutus
Tiuclaenus n.sp. 1
Tiuclaenus n.sp. 2
Pucanodus gagnieri
Family MIOCLAENIDAE or DIDOLODONTIDAE
Mioclaenidae or Didolodontidae n.g., n.sp.
Andinodus boliviensis
Family ? PERIPTYCHIDAE
aff. ? *Mimatuta*
Order CONDYLARTHRA *incertae sedis*
Family KOLLPANIIDAE
Kollpania tiupampina
Order NOTOUNGULATA
Family HENRICOSBORNIIDAE or OLDFIELTHOMASIIDAE

The age of the fauna is now commonly accepted to be Palaeocene (Gayet *et al.* 1992; Muizon 1992; Muizon & I. Brito 1993; Marshall *et al.* 1995) contrary to the Late Cretaceous age initially assigned to the Tiupampa mammals (Marshall *et al.* 1983; Muizon *et al.* 1983; Marshall *et al.* 1985; Marshall & Muizon 1988).
The position of the Tiupampa (site 1) mammal fauna within the Palaeocene has been discussed by Van Valen (1988), Muizon & I. Brito (1993), Bonaparte *et al.* (1993), and Marshall *et al.* (1995) and assigned an early Palaeocene age. According to these authors, the Tiupampian (early Palaeocene) local mammal fauna (type locality: site 1 at Tiupampa) is older than the Peligran local mammal fauna (type locality: Punta Peligro, Patagonia, Argentina) (Muizon & I. Brito 1993; Bonaparte *et al.* 1993: 36, 37; Bonaparte & Morales 1997). The relative age of the faunas is based on the comparison of the evolutionary stage of the condylarths they have yielded. Although this approach is certainly questionable, it is obvious that the three condylarths of the Punta Peligro fauna are more derived than the relatively generalised forms of Tiupampa (six genera). Furthermore, a new ungulate from Punta Peligro (Bonaparte & Morales 1997) shows a clearly prelophodont morphology which recalls, although more primitive, *Notonychops* from the Rio Loro Formation of northern Argentina (Soria 1989). The Punta Peligro fauna has been found in the Banco Negro Inferior and its age is early Palaeocene. It probably spans from 63.2 to 61.8 Ma, as stated by Pascual & Ortiz-Jaureguizar (1992: 564), who provided a review of the age of the Banco Negro Inferior. The Tiupampa local fauna is here regarded as older than the Punta Peligro fauna and, therefore, if the date of the base of the Banco Negro inferior is correct, the Tiupampa fauna is older than 63.2 Ma. Therefore, according to Haq & Van Eysinga (1994), it would be pre-Torrejonian in age and contemporaneous with the Puercan. The Punta Peligro fauna is probably contemporaneous with the Torrejonian of North America. I therefore agree with the gross equivalence, proposed by Bonaparte *et al.* (1993), of the Tiupampian with the Puercan and the Peligran with the Torrejonian.
Recently, Marshall *et al.* (1997) and Sempere *et al.* (1997) have correlated the Tiupampa beds to the

magnetic anomaly chron 26r which would correlate the Tiupampian land mammal age with the early Tiffanian North American land mammal age (*i.e.* early late Palaeocene). However, the pantodonts and condylarths (groups that can be compared in both subcontinents) of the Tiffanian faunas of North America are much more derived and more diverse than those of Tiupampa and clearly seem to represent a younger fauna. Furthermore, since the entire series of the Santa Lucía Formation at Tiupampa corresponds to a (possible?) single reversed chron, the correlation of the Tiupampa beds with the other Maastrichtian-Palaeocene series of Bolivia (La Palca, see Marshall *et al.* 1997) has been based on lithological facies and sedimentological sequences. Marshall *et al.* (1997) include the mammal bearing beds at Tiupampa in the middle sequence of the Santa Lucía Formation, which they have correlared with the last sequence of the underlying El Molino Formation to the chron 26r. However, the authors have not presented the sedimentological arguments which allow the suggested correlation and the sedimentology and depositional environment at Tiupampa are neither described nor discussed.
Furthermore, some basic considerations seriously weaken the correlation proposed by Marshall *et al.* (1997) and Sempere *et al.* (1997): (1) the Tiupampa series is located on the edge of the El Molino-Santa Lucía Basin and therefore the sedimentation may be atypical and may have very local characteristics; this observation obviously makes correlations based on sedimentological data very hazardous; (2) the Tiupampa beds were deposited on an alluvial plain, an environment which is generally characterized by an irregular rate of sedimentation; (3) several paleosols with root casts have been mentioned at Tiupampa (Muizon *et al.* 1983) which could correspond to important interruptions in the sedimentation. For example, the single reversed interval of Tiupampa could very well correspond to chron 27r and 26r with lack of sedimentation, or erosion of sediments corresponding to chron 27n. Since no radiometric dates are available, so far, at Tiupampa, this difficulty cannot be resolved; (4) although considerably improved during the last fifteen years, the knowledge of the Late Cretaceous and Palaeocene of Bolivia is still very incomplete, a statement to which must be added general considerations concerning the variability of the rates of sedimentation and the great difficulty in determining the importance of sedimentation gaps.
Furthermore, at Vila Vila, at about 5 km east of Tiupampa, in the same outcrop, a Maastrichtian fish fauna (Gayet *et al.* 1992: 400) indicates the presence of Maastrichtian beds of the El Molino Formation (probably belonging to the lower sequence of the formation). Those beds have a facies of mainly thick red sandstones corresponding to a more detrital sedimentation, uncommon for the El Molino Formation and probably indicative of the local border of the basin, which could explain the atypical facies found at Vila Vila and Tiupampa.
In spite of Marshall *et al.* (1997)'s claim of having the only acceptable approach to the relative chronology, the correlation they suggested of the Tiupampa beds to the early Tiffanian is still weakened by numerous unknowns and approximations. Their age assignment is certainly not convincing (as far as the mammal fauna is concerned) and, in spite of the appearances of a rigorous quantitative analysis, it is not more objective than a faunistic approach, which, as mentioned above, presents the uncertainties that everybody knows. Marshall *et al.* (1997) may be correct (although it would be extremely surprising) in assigning a Tiffanian age to the Tiupampa beds, however they failed to demonstrate it.
Therefore, on the basis of faunistic comparisons, the age correlation of the Tiupampa mammal fauna to the Puercan is still accepted here, following Van Valen (1988), Bonaparte *et al.* (1993), Muizon & I. Brito (1993), Marshall *et al.* (1995) and Bonaparte & Morales (1997).

DESCRIPTION

Serial designation for teeth follows Luckett (1993) *contra* Archer (1978), Hershkovitz (1982), Marshall & Muizon (1988) and Muizon (1992), *i.e.* premolars are P1, P2, P3; deciduous tooth is dP3; permanent molars are M1, M2, M3, M4; terminology for molar structure follows Marshall & Muizon (1995); usage of Metatheria follows Szalay (1994) and Szalay & Trofimov (1996); usage of Theria follows Kielan-Jaworowska *et al.* (1987), and Tribosphenida follows McKenna (1975); suprageneric ranks of Metatheria follow Marshall *et al.* (1990). All measurements are in millimetres (mm).
Abbreviations of teeth are as follows: c, lower canine; C, upper canine; i, lower incisor; I, upper incisor; m, lower molar; M, upper molar; p, lower premolar; P, upper premolar.
Anatomical elements are described in the following order: upper dentition, lower dentition, skull, dentary, vertebrae, forelimb and hindlimb. When necessary to the understanding of the text, the description will include some comparisons, mainly with the other borhyaenoids and/or with didelphids. In the following description of the dentition of *Mayulestes ferox*, comparisons will be made essentially with two borhyaenoids

(*Allqokirus australis* from the same locality and *Patene simpsoni* from the early late Palaeocene of Brazil) and with *Deltatheridium praetrituberculare*, a tribosphenidan from the Late Cretaceous of Mongolia.

SKULL

The dental formula of *Mayulestes ferox* is the complete primitive marsupial formula: I5/i4; C/c; P3/p3; M4/m4 (Owen 1868, but see also Luckett 1993).

Upper dentition

Upper incisors. (Fig. 1) The number of upper incisors is not reduced to four as in other borhyaenoids. However, it is noteworthy that the number of incisors is unknown in *Allqokirus*, *Patene* and *Nemolestes*, three other Palaeocene borhyaenoids. The incisor tooth row is parabolic and differs from the straight (or slightly concave posteriorly) row observed in Miocene borhyaenoids (*Cladosictis*, *Sipalocyon*, *Prothylacynus*, *Acrocyon*). In the holotype of *Mayulestes*, the left I1 is not preserved and the crowns of the left I2 and right I3 are broken. I1 is the largest incisor. In diameter of the crown I1 > I2 < I3 > I4 > I5. The crown of I1 is conical, slightly recurved posteriorly and approximately twice as high as wide at the base. The apex of the crown of I2 is broken; this tooth is the second smallest upper incisor in diameter. The section of the crown is subcircular, slightly flattened labiolingually. The anterior base of the crown is protruding anteriorly. The I3 has a much lower crown than the I1; it is triangular in labial view and clearly flattened labiolingually. The crown of I3 is protruding anteriorly and posteriorly slightly below the junction with the root. The mesiodistal diameter of the crown is only slightly smaller than its height. The I4 has a much smaller crown than the I3. It is triangular in labial view. Its maximum mesiodistal diameter is also located below the crown-root contact but, contrary to I3, it is slightly larger than the height of the crown. The I5 is the smallest of the upper incisors. The crown is conical and not constricted at the contact with the root. The labial edges of the alveoli of I1-4 are at the same level while that of I5 is situated a little more dorsally at the anterior edge of a large ptemaxillomaxillary fossa for the tip of the lower canine. There is no true diastema, although I1-4 are not as close to each other as I4 and I5. A distinct diastema separates I5 from C.

Upper canine. (Fig. 1) The tooth is large, pointed and slender. It is complete on the right side only where it has been partially expelled from its alveolus during fossilization. The right C therefore appears to be longer than it probably was on the living animal. The crown is less than half of the length of the observable portion of the tooth. It bears an important anterior wear facet for the lower canine, which continues dorsally on the root. In cross-section, the tooth is ovoid, being





FIG. 1. — *Mayulestes ferox*, holotype (MHNC 1249). Anterior part of the palate with incisors canines and anterior premolars. Scale bar: 1 cm.

longer than wide (l: 4.9 mm; w: 1.9 mm). The tooth is recurved posteriorly but to a lesser extent than in *Pucadelphys*, as the tip of the crown is anterior to the level of the posterior edge of the alveolus. It approaches the condition observed in *Sipalocyon*, although it is approximately 40% smaller.

Upper premolars. (Fig. 2) The three upper premolars of *Mayulestes* are double-rooted. The size of the teeth increases from P1 to P3. P1 is considerably smaller than the other premolars. The difference in size between P1 and P2 is more important than in other borhyaenoids and *Pucadelphys* but approaches the condition observed in *Deltatheridium*. P1 has a tiny single-cusped asymmetrical crown. In labial view, its posterior edge is strongly oblique (in relation to the alveolar border) and rectilinear while the anterior edge is subvertical and convex anteriorly. At the base of the posterolabial edge of the crown is a minute cuspule. P1 is set slightly obliquely in the maxilla, as observed in *Pucadelphys* (Marshall & Muizon 1995) and *Andinodelphys* (Muizon *et al.* 1997). However, the obliquity of the left P1 has probably been increased by the deformation due to fossilization. The crown of the P2 is triangular and longer than high in labial view. In occlusal view, it is flattened transversally. It presents a small cuspule at its anterior base and a conspicuous cusp at its posterior base. The apex of the crown lies ventrally below the posterior edge of the anterior root. The cristae running from the apex to the basal cusps are straight and the posterior is longer than the anterior. The P3 is the highest of the cheek-teeth. It is a little longer than P2 and much higher. The difference between the proportions of P2 and P3 is more important in *Mayulestes* than in *Pucadelphys* and the other borhyaenoids but resembles the condition observed in *Deltatheridium*. The crown of the P3 is clearly higher than long, as in *Pucadelphys*, *Patene* and *Sipalocyon*. The anterior edge of the crown is a smooth crista, convex anteriorly and possessing a small heel at its base. The posterior edge is a well marked crista, concave posteriorly with a well-defined cusp at its base. The apex of the crown lies ventrally to the anterior edge of the posterior root and, in lateral view the crown is slightly recurved posteriorly. On P2 and P3 there is a small posterolabial cingulum which disappears anteriorly.

Upper molars. (Fig. 2) In the only specimen known, the molars are slightly worn but the dental morphology is clearly recognisable. In length, M1 < M2 > M3 > M4 and in width M1 < M2 < M3 > M4 (Table 1). The molars of *Mayulestes* are relatively shorter anteroposteriorly than in *Allqokirus* and *Patene*. On M1-3 the protocone is relatively large for a borhyaenoid but narrow anteroposteriorly and slightly inflated basally, especially on its posterior side. In *Allqokirus*, a borhyaenoid from the same locality, the protocone is even shorter anteroposteriorly and not inflated basally; the protocone of *Mayulestes* is shorter than in *Patene*. The protocristae are straight; the preprotocrista is slightly shorter than the postprotocrista and, as a consequence, the apex of the protocone is located in an anterior position on the cusp. The trigon is well basined. The conules are small but well marked; they are distinctly V-shaped and well separated from the paracone and metacone as observed in *Allqokirus*. Because of the slight wear of the teeth it is not possible to determine with certainty the relative size of the conules. A distinct paracingulum unites the preparaconule crista to the stylar cusp A. In fact, the paracingulum is continuous with the preparaconule crista as in *Allqokirus* and *Patene*. The para- and metacone are well-developed, well separated and constitute the central cusps of the molars. The metacone is slightly compressed transversally, this being particularly obvious on M3 as in *Allqokirus*. It is distinctly larger in height and volume than the paracone. In occlusal view, the paracone is approximately 30% shorter and narrower than the metacone. On the four molars the paracone is more worn than the metacone and on M3 the paracone is relatively worn while the metacone is almost unworn. In spite of this, the difference in height of the two cusps is so important that it is clear that the paracone was lower than the metacone. The centrocrista is straight in occlusal view. In labial view, the centrocrista is deeply V-shaped and presents a notch at the junction point of the premetacrista and postparacrista. From this point, the highest of the centrocrista, a deep

groove runs labially dividing the stylar shelf transversally but not reaching the labial cingulum. The same condition is observed in *Allqokirus* and, to a lesser extent, in *Patene*. The preparacrista links the paracone to the stylar cusp B. It is transverse, almost perpendicular to the centrocrista. On M1-2, it is slightly concave posteriorly. On M3-4, it is slightly worn but it seems that it was almost straight. It is distinctly concave ventrally in anterior view. Its length increases from M1 to M4 where it is almost three times longer than on M1. The postmetacrista is well-developed and relatively long but fairly low. It is approximately twice as long as the preparacrista on M1-3. It is almost straight in occlusal view and slightly concave in posterior view. On M1, it forms an angle of approximately 45° with the anteroposterior axis of the skull; this angle increases on M2 and it reaches almost 80° on M3. Posterior to the preparacrista and anterior to the postmetacrista, the stylar shelf bears two elongated fossae directed posterolabially and anterolabially, respectively. Similar structures are observed in *Allqokirus* and *Patene*. The stylar shelf is similar to that of *Allqokirus* but it is larger and deeper than in *Patene*. It differs from the condition in other borhyaenoids, where the stylar shelf is either very reduced or, generally, totally absent. Its width increases from M1 to M3. The stylar cusps are relatively well-developed with the exception of stylar cusp C, which is absent. Stylar cusp A is medium-sized on M1-2 and distinctly lower than stylar cusp B. The two cusps are connate but easily discernible. On M3, stylar cusps A and B have the same height and are connate but not totally fused. On M4 they are fused. The stylar cusps A and B of *Patene* are smaller than in *Mayulestes* but their relative size and relationship are similar. The stylar cusps A and B of the M3 of *Allqokirus* (the only molar known) are similar to those of *Mayulestes*. As mentioned above there is no stylar cusp C in *Mayulestes* as in *Allqokirus* and *Patene*. In these three genera, there is a distinct labial cingulum in the stylar cusp C position. The stylar cusp D is well-developed in *Mayulestes*, contrary to *Allqokirus* where it is very small and *Patene* where it is absent. In *Mayulestes*, a small crista runs lingually from the cusp within the basin of the stylar shelf, but does not reach the postmeta-

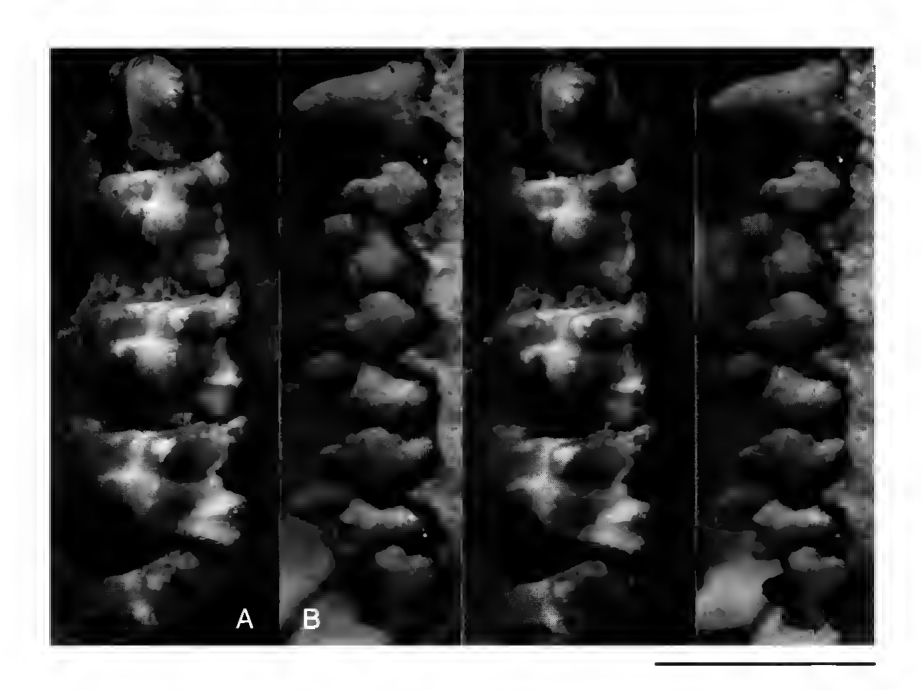


FIG. 2. — *Mayulestes ferox*, holotype (MHNC 1249). Left upper molars and premolars: **A**, occlusal; **B**, labial views. Scale bar: 5 mm.

crista or the metacone. This crista is absent in *Allqokirus* and *Patene*. The stylar cusp E is small as in most marsupials and in fact constitutes the labial extremity of the postmetacrista. On M1-3 the ectoflexus is very deep and its depth increases from M1 to M3. It is deeper than in *Allqokirus* and much deeper than in *Patene* and *Sallacyon*. An ectoflexus is absent or extremely reduced in the other borhyaenoids.

The M4 is very short anteroposteriorly (much shorter than in *Patene*) but still retains a metacone as in *Patene* and *Sallacyon* (it is tiny in this genus), contrary to the other borhyaenoids. The trigon is still well basined and the stylar shelf is reduced but present. The stylar cusps A and B are totally fused in a very large "parastyle"; there is just a hint of stylar cusp D and the stylar cusp E has totally disappeared.

Lower dentition

Lower incisors. (Fig. 3) In the description of the lower incisors of *Mayulestes* the medial incisor will be regarded as the i2 and the lateral as the i5 following Hershkovitz (1982). The four incisors are preserved on the right dentary only. Their relative volume in occlusal view is as follows: i2 < i3 > i4 > i5. The incisors have a single cusped crown. The i2 is slightly compressed mesiodistally and i3-5 are compressed labiolingually, i4 and i5 being clearly spatulate. The incisor row is a regular arch but the root of i3 is staggered and buttressed labially as observed in most didelphids, several borhyaenoids (*Borhyaena*, *Siaplocyon*, *Cladosictis*, *Thylacinus*), some dasyurids and peramelids (Hershkovitz 1982). A staggered i3 is also present in *Pucadelphys* and *Andinodelphys* (Muizon *et al.* 1997).

Lower canine. (Fig. 3) The lower canine is large although conspicuously smaller and shorter than the upper canine. It is longer than wide and compressed transversally (this is particularly clear on the root). The large axis of the tooth is set at an oblique angle in relation to the cheek tooth series. It is gently recurved posteriorly and its posterior edge bears a distinct wear surface from the upper canine.

Lower premolars. (Fig. 3) The p1 is only preserved on the right hemimandible; the posterior heel of the p2 and complete p3 are preserved on the left hemimandible. The three premolars are double rooted. The p1 is very small, single cusped and triangular. It is set slightly obliquely in the dentary, as in the Borhyaenidae (although this feature is much more emphasised in the representatives of this family). In labial view the posterodorsal edge of the crown is three times longer than the anterodorsal. Therefore, the tooth is strongly asymmetrical and its apex is displaced anteriorly and occurs above the middle of the anterior root. The anterior edge of the crown overhangs the anterior border of the anterior root. The p2 is known by its posterior heel only, which is similar in size with that of p3. The p3 has a high crown. It is higher than long, as in *Patene* and *Sipalocyon* but contrary to *Cladosictis*. As in *Patene*, the apex of the tooth is located above the anterior root, contrary to *Cladosictis* and *Sipalocyon* where it is located above the middle of the tooth. The anterior edge of the main cusp is convex and the posterior edge concave; the former is approximately 40% shorter than the latter. Because of the shape of its edges, the main cusp of the tooth is slightly recurved posteriorly. In occlusal view, the labial side of the main cusp is strongly convex while the lingual side is relatively flat. The anterior edge of the tooth has no basal cusp but the anterior base of the crown protrudes anteriorly and is elevated. The concave area below the protruding base of the crown receives the posterior heel of the p2. Such a condition is also observed in *Patene* and in most didelphids. It is absent in other borhyaenoids where the cheek tooth row is less compressed anteroposteriorly. There is no diastema between the canine and p1 and between the premolars.

Lower molars. (Figs 3, 4) In length and height m1 < m2 < m3 < m4 and in width of the trigonid m1 < m2 < m3 > m4. However, the increase in size is moderate, contrary to the condition in most other borhyaenoids. The lower molar structure is similar to that of *Allqokirus* but the tooth proportions are more slender and the m3 of *Mayulestes* (the only lower molar known in *Allqokirus* is an m3) is smaller and narrower than that of *Allqokirus*. Besides the size, the main difference between anterior and posterior molars is the shape of the trigonid in occlusal view, which

becomes wider and less opened lingually from m1 to m4. On the four molars the trigonid is much higher and wider than the talonid. The protoconid is very large and is much higher than the other cusps of the trigonid. It has a triangular section and is swollen labially while the lingual side is flat. This morphology is commonly observed among borhyaenoids but is better marked in *Mayulestes*, *Allqokirus*, *Patene* and *Nemolestes* than in the other borhyaenoids. The paraconid is similar in proportion to that of *Patene*, but is smaller than in most other borhyaenoids. It has a triangular section in occlusal view. On the anterolingual edge of the

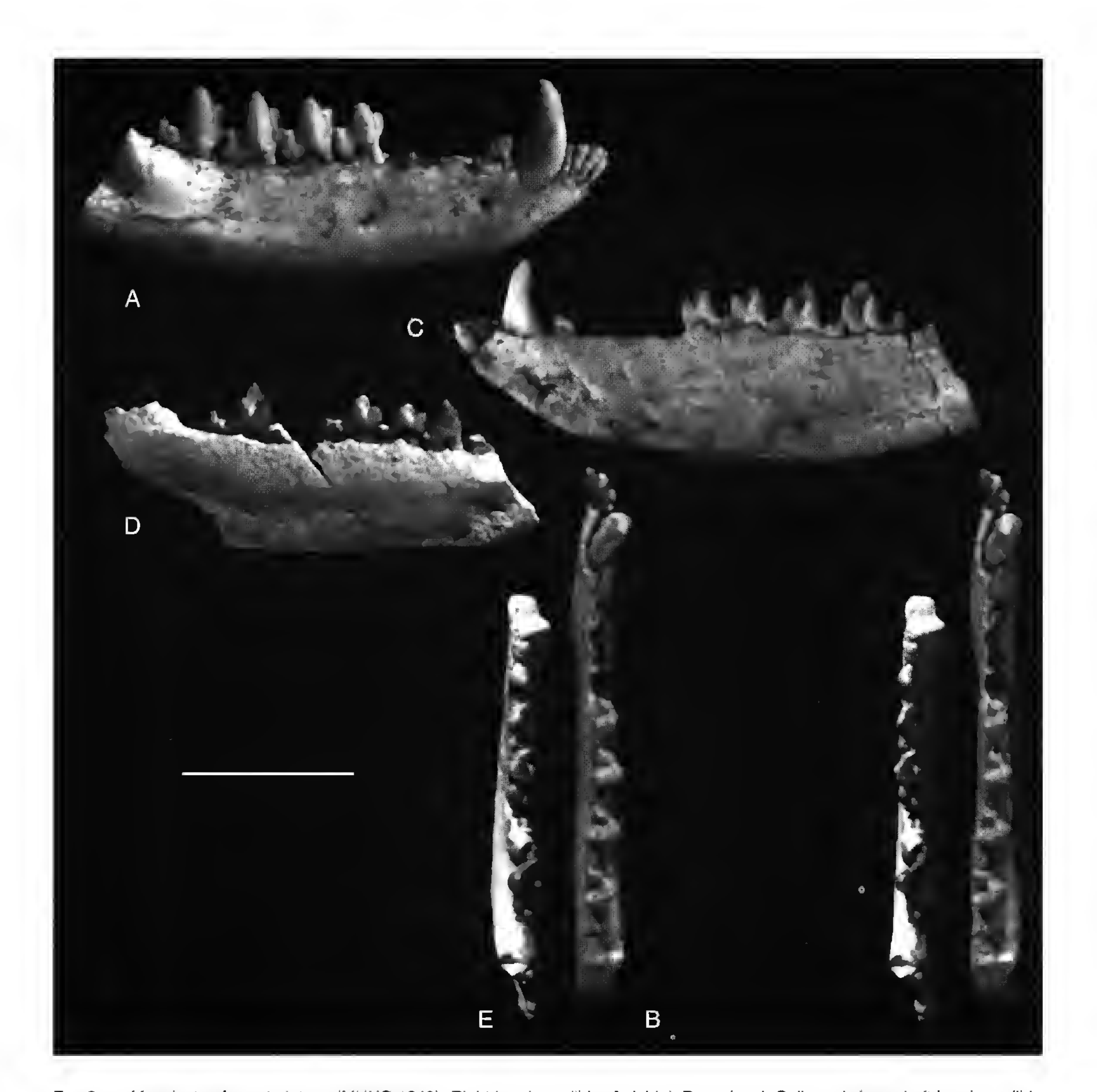
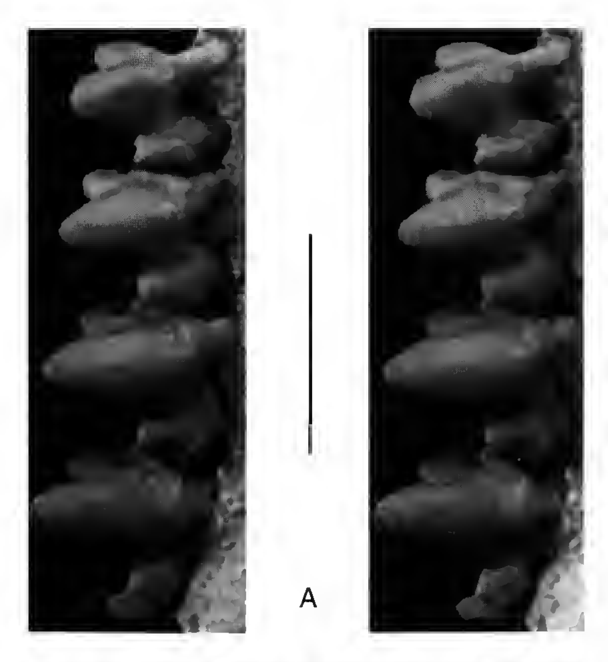


FIG. 3. — *Mayulestes ferox*, holotype (MHNC 1249). Right hemimandible: **A**, labial; **B**, occlusal; **C**, lingual views. Left hemimandible: **D**, lingual; **E**, occlusal views. Scale bar: 1 cm.

paraconid is a large, salient preparacristid, appressed against the lingual side of the hypoconulid of the preceding tooth. In fact the latter interlocks with the anterior edge of the following tooth. The anterolingual side of the paraconid is concave and receives the preceding hypoconulid which is limited lingually by the paracristid and labially by the lingual edge of the precingulid. This feature is likely to be plesiomorphic since it is observed in all the other borhyaenoids (although somehow altered in forms with very robust dentitions), in didelphids, in several Cretaceous Theria (*Kielantherium*, *Asioryctes*, *Prokennalestes*, *Kokopellia*, *Eodelphis*, *Didelphodon*, *Alphadon*, *Glasbius*) and in the eupantothere *Peramus*.



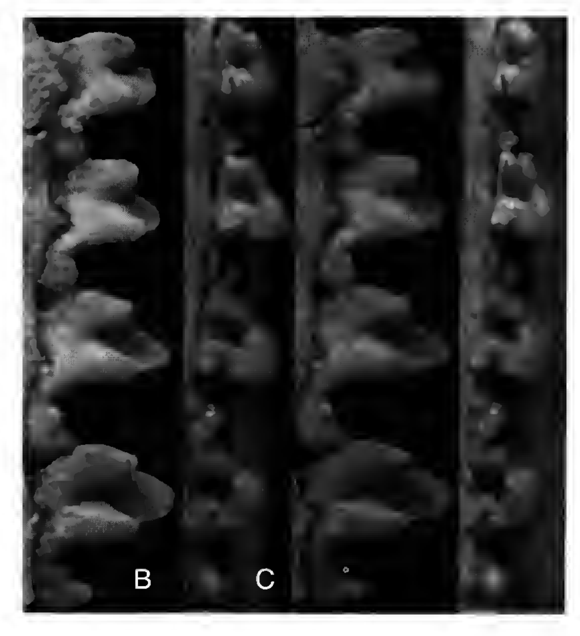


Fig. 4. — *Mayulestes ferox*, holotype (MHNC 1249). Right lower molars: **A**, labial; **B**, lingual; **C**, occlusal views. Scale bar: 5 mm.

When unworn (*i.e.* on m4), the paraconid and the metaconid are subequal in height. The metaconid is slightly less robust and shorter in lingual view than the paraconid. It has a subcircular section in occlusal view and is relatively large for a borhyaenoid. It resembles in size those of *Allqokirus* and *Patene* (although, in the latter genus, it is sometimes slightly smaller than the paraconid), but it is larger than in all the other borhyaenoids which still retain a metaconid (*Nemolestes*, *Pharsophorus*, *Plesiofelis*). In these genera the metaconid is always much smaller than the paraconid. The paracristid and protocristid are sharp and show a conspicuous carnassial notch at the limit of the cusps (respectively paraconid and protoconid; protoconid and metaconid). The protocristid is almost transverse while the paracristid is strongly oblique in relation to the tooth row (the obliquity is more pronounced in the anterior than in the posterior molars). At the anterolabial base of the trigonid is a strong precingulid which runs from the labial angle of the paraconid to the base of the protoconid above the middle of the anterior root.

The talonid is narrower than in *Allqokirus*, *Patene*, *Sipalocyon* and *Cladosictis*. The basin of the talonid is moderately developed and opens lingually between the entoconid and the metaconid. The talonid is characterized by the large size of its hypoconid and the great reduction of its entoconid. The hypoconid is the largest cusp of the talonid. It is much larger than the entoconid and more voluminous than the hypoconulid. Although it is slightly worn on the specimen described, on m1-3 it was probably as high as the hypoconulid and slightly lower on m4. The entoconid is very small and much less volumi-

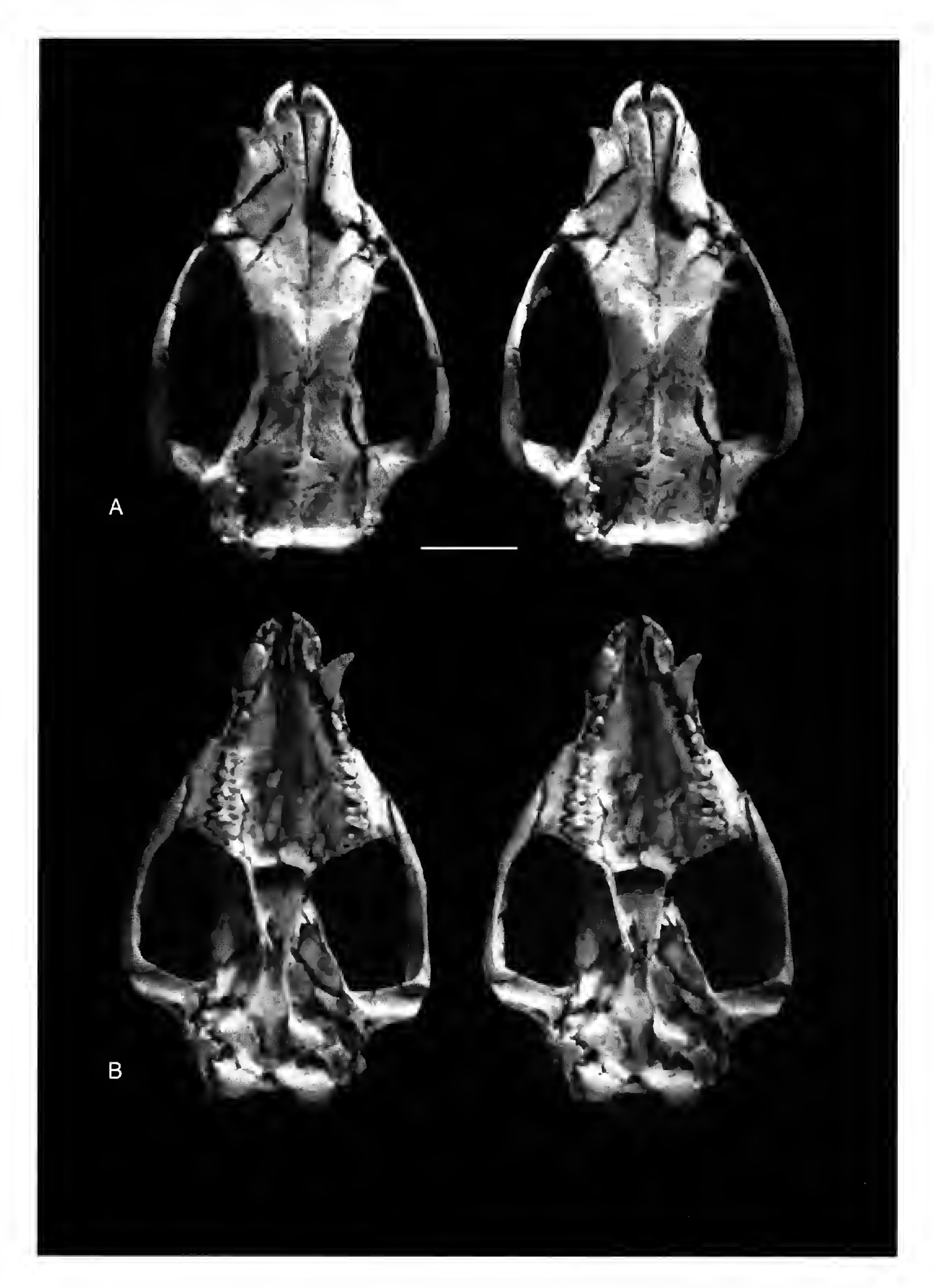
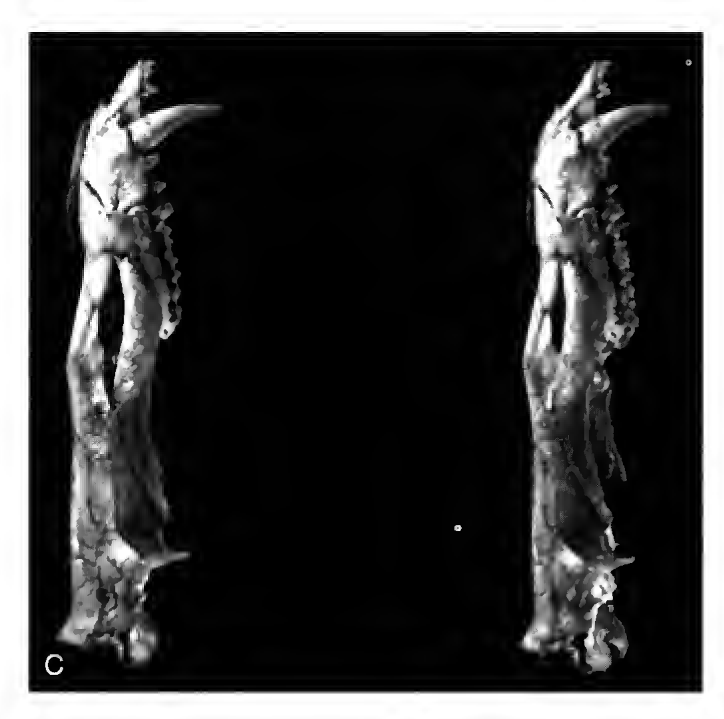


FIG. 5. — *Mayulestes ferox*, holotype (MHNC 1249). Skull: **A**, dorsal; **B**, ventral; **C**, lateral views. Scale bar: 1 cm.



nous and lower than the hypoconid. In this respect, it resembles the condition observed in *Allqokirus* but differs from *Patene* where the entoconid (although less voluminous than the hypoconid) is less reduced than in *Mayulestes* and has approximately the same height (sometimes it is higher) as the hypoconid. A well-developed cristid obliqua connects the anterolingual angle of the hypoconid to the posterolingual angle of the protoconid slightly labial to the notch of the protocristid. The hypoconulid is moderately large on m1-2 where it is only slightly higher than the entoconid. On m3-4 it is voluminous and high. On the four molars it is very salient posteriorly, contrary to the other borhyaenoids. It is located in a lingual position but not connate to the entoconid. This condition is probably due to the great reduction of the entoconid, since this feature is very clear on the other borhyaenoids. On m1-3 a large postcingular shelf extends ventrolabially from the tip of the hypoconulid across the posterolabial surface of the hypoconid. The postcingulid is very reduced on m4 and does not reach the tip of the hypoconulid.

Bony skull

General features. (Figs 5, 6) The only skull known of *Mayulestes* is dorsoventrally crushed, but it is probable that it little affected the ventral and dorsal views of the skull. The major damage to the skull is in the basicranium where the basioccipital, the basisphenoid and the alisphenoid have been pushed down into the braincase (the skull has fossilised with the palate facing dorsally). The petrosals, the glenoid fossae and the occipital condyles have resisted the pressure better and remained salient. The skull is small and relatively short anteroposteriorly when compared to gracile forms such as *Cladosictis* and *Sipalocyon*. It is not as stout as that in *Borhyaena* and approaches the proportions observed in *Prothylacynus*. Although the rostrum seems to be shorter than in other borhyaenoids, Table 1 (p. 86) shows that the ratio of length of the rostrum (from the tip of the premaxillae to the anterior foramen of the infraorbital canal) to total length of the skull is higher in *Mayulestes* than in any Santa Cruz borhyaenoids. The rostrum of *Mayulestes* does not have the strong postcanine constriction observed in the

Santa Cruz borhyaenoids and, in this respect, it clearly resembles the morphology observed in didelphids. The temporal fossae are long and represent more than half of the skull length. The maximum width of the skull is located at the posterior extremity of the temporal fossae, slightly anterior to the glenoid fossae. The zygomatic arches are regularly curved from their anterior root to the glenoid cavity, where they form an almost right angle before contacting the braincase. This condition is similar to that observed in *Borhyaena*, *Cladosictis* and *Prothylacynus*, but differs from that in *Sipalocyon* where the zygomatic arch is regularly convex from its anterior to its posterior root and where the maximum width of the skull is more anterior. The interorbital constriction is weak and has a width close to that of the temporal fossa. In all other borhyaenoids it is clearly narrower. The braincase is large and not clearly separated from the interorbital bridge. Its lateral edges are almost straight, regularly divergent posteriorly and not convex as in other borhyaenoid skulls.

A small but well marked sagittal crest is present. It begins on the posterior edge of the frontals, runs posteriorly on the parietals and rises at its contact with the lambdoid crest. It is low and has the same elevation all along the parietal. The posterior part of the braincase shows a well-developed dorsoposteriorly directed lambdoid crest. Both the sagittal and lambdoid crests are more reduced than in the other borhyaenoids and the lambdoid crest does not overhang the occipital condyles posteriorly.

In ventral view, the palate is wide and the dental rows are straight to convex laterally, contrary to other borhyaenoid where they are generally concavo-convex. The glenoid fossa is located posteriorly, lateral to the anterior extremity of the promontorium of the pars petrosa and to the foramen ovale. The latter is located at the posteroventral angle of the alisphenoid. Its anterior border is formed by the alisphenoid and its posterior edge is formed by the petrosal.

Nasal. (Figs 5A, 6A) The bones extend anteriorly beyond the anteriormost point of the nasal-premaxilla suture. The anterior halves of the nasals are elongate and narrow. They become progressively narrower posteriorly and are narrowest at the level of a transverse line joining the anterior foramina of the infraorbital canal. Posterior to this line, they strongly and rapidly widen and reach their largest width at the triple junction with the frontal and the lacrimal where they form a small posterolaterally directed horn. The frontal-nasal suture is markedly W-shaped, with the base of the W facing posteriorly. The nasals of *Mayulestes ferox* have a clear contact with the lacrimal, a plesiomorphic feature observed in all other borhyaenoids.

Premaxilla. (Figs 5, 6) The anterior edge (the alveolar border) of the premaxillae is gently arched when viewed dorsally or ventrally and the bones protrude anteriorly contrary to what is observed in other borhyaenoids, where the anterior edge of the premaxillae is almost straight and transversal. As a consequence, the incisor tooth row, in ventral view, is a wide open parabola while it is generally straight in other borhyaenoids. The ascending process of the premaxilla is long and slender and inserts between the nasal and the maxilla posterodorsally. The length of the premaxilla-nasal suture is approximately 25% of the total length of the nasal. The width of the ascending process is roughly constant from its anteroventral extremity to the anterior point of the nasal-premaxilla suture. This part of the process, approximately half of it, forms the lateral edge of the external nares. The posterior half of the process articulating with the nasal is very sharp and progressively tapers posteriorly.

At the anterior point of the nasal-premaxilla suture the anterodorsal border of the ascending process shows a distinct anterodorsal protrusion which corresponds to the point of junction between the plane of the external nares and the dorsal surface of the rostrum. The two planes form an angle of approximately 140°. Laterally, the maxilla-premaxilla suture runs anteroventrally and reaches the alveolar border slightly beyond the upper canine and the bottom of the fossa for the lower canine. In this fossa the maxilla-premaxilla suture runs posteromedially and reaches the lingual alveolar border at the anteromedial angle of the canine. At this point the suture takes an almost anteroposterior direction.

On the lateral border of the canine fossa, the

premaxilla is in contact with the anterolateral process of the maxilla which forms the posterior third of the lateral wall of the canine fossa. Its two anterior thirds are formed by the premaxilla itself. In other borhyaenids, the maxilla forms no part of the lateral border of the fossa for the lower canine while in the didelphids and in *Pucadelphys* (early Palaeocene of Bolivia) the maxilla forms the entire lateral wall of the fossa. The borhyaenoids are characterized by the loss of the maxillary anterolateral process which borders the canine fossa laterally. The condition of *Mayulestes* represents an incipient development of this borhyaenoid feature, since the anterolateral process of the maxilla is greatly reduced when compared to the didelphoids but has not totally disappeared as is observed in the other borhyaenoids. The fossa for the inferior canine is located anterior to the upper canine. Its anterior part is in the premaxilla just behind and dorsal to the I5. The bottom of this fossa is in the small portion of the maxilla, anterolateral to the upper canine and its lateral rim is formed by the maxilla. Its dorsal extremity is situated more ventrally than in *Cladosictis*, *Sipalocyon*, *Acrocyon*, and *Borhyaena*. The incisive foramina are elongated, narrow and slightly concave laterally. Their anterior extremity is at the level of the posterior end of the I3 and their posterior end reaches the anterior border of the canine. The medial edges of the incisive foramina are made of the ventromedial processes of the premaxillae, which seem to diverge slightly posteriorly. It is also possible that the divergence of the processes is the result of the deformation of the skull due to fossilization.

Maxilla. (Figs 5, 6) The dorsal process of the maxilla is a low rounded blade, articulating anteriorly with the premaxilla, dorsomedially with the nasal, posteriorly with the lacrimal and laterally with the jugal. It has no contact with the frontal. The posterior edge of the dorsal process has a transverse suture that is roughly convex anteriorly. It articulates laterally with the jugal at the level of the anterior part of M2 and passes on the ventral side of the skull. The jugal-maxilla sutures are almost parallel to the alveolar border, slightly converging anteriorly. The anterior opening of the infraorbital canal opens dorsal to P3. It is of moderate to small size and probably slightly elongated dorsoventrally. This observation is difficult because of the crushing of the skull. The posterior opening is flattened by deformation but it is likely that it was elongated transversally. It opens dorsal to M2. Its dorsal rim is formed by the lacrimal and its ventral rim by the maxilla. It is not possible to determine if, as in *Pucadelphys*, the palatine also participates to the medial rim of the foramen. In Recent metatherians, the infraorbital canal transmits the infraorbital branch of the V2, a branch of the infraorbital artery and a small vein (Archer 1976). The floor of the orbit is formed by the maxilla. Its suture with the palatine, medially, is not observable.

On the ventral side of the palate, there is a large postpalatine foramen with an orientation similar to that observed in *Didelphis*. It faces anteromedially with a small ventral component. Because of this condition, in ventral view, the postpalatine foramen appears as an elongated slit with an anterolateral-posteromedial orientation. This is clear on the left side of the specimen where the foramen is intact. The postpalatine foramen of *Mayulestes* is proportionally much larger than in other borhyaenoids. Its anterolateral edge is formed by the maxilla and its dorsal, ventral and posteromedial edges are formed by the palatine. The palatine-maxilla suture is difficult to determine but it probably formed a regular parabola with an apex at the level of M1 and with branches reaching the anterior border of the postpalatine foramen. Although the palate has been deformed it is possible to observe that it was fairly deep and hollowed. The palatal portion of the maxilla has no vacuities.

The anterior extremity of the maxillae on the palate shows two small anterolateral processes which form the posterolateral rim of the incisive foramina. On its anteromedial edge each maxilla shows a tiny anteromedial process wedged between the ventromedial process of the premaxilla and the vomer.

Palatine. (Figs 5, 6) On the posterior extremity of the palate, the ventral edge of the choanae is relatively wide. It is approximately half of the distance between the protocones of the M4 while it is close to one third of the distance in *Borhyaena*, *Prothylacynus*, *Cladosictis* and

Sipalocyon. The edge is thickened but does not form a true postpalatine torus as observed in most didelphoids (including *Pucadelphys*, the oldest member of the superfamily known from skulls and skeletons), where it is salient ventrally and laterally. In this respect it resembles the condition observed in other borhyaenoids and differs from that in the didelphoids. In anteroventral view of the palate the ventral rim of the choanae is markedly concave ventrally. At the interpalatine suture, a median spine is formed by the two medial spines of each bone. A lateral spine is located on the posterior edge of the postpalatine foramen and oriented ventrally. It articulates with the anterior extremity of the pterygoid wing and is closely appressed to it. It also articulates with the maxilla anteriorly. The lateral spine and its articulation with the pterygoid are located ventrally to the medial spine. Although the palatine bones are broken, it is possible to observe that they had no palatal vacuities a condition found in all the other borhyaenoids.

The orbital portion of the palatine is badly damaged because of the crushing of the skull, and, therefore, its relationships with the lacrimal and the maxilla are very difficult to observe. However, on the right side of the specimen, a large sphenopalatine foramen, opening posteriorly, is located ventrally and slightly posterior to the lateral extremity of the frontal-lacrimal suture. It is well anterior to and dorsal to the postpalatine foramen. The sphenopalatine foramen transmits the sphenopalatine artery and nerve into the nasal cavity.

Posteromedially, the palatines have two large sphenoidal processes which roof the choanae and the palatine gutter. The processes underlap the presphenoid and the basisphenoid and have a small contact with the anterior processes of the alisphenoids. This condition is probably similar to that observed in the didelphids.

Pterygoid. (Figs 5C, 6C) Both pterygoids are preserved on the specimen described here. The pterygoid of *Mayulestes* is a large (for a borhyaenoid), triangular blade, located lateral to the roof of the choanae. It is high and has a well-developed hamulus on its posteroventral extremity. It articulates mostly with the posteromedial extensions of the palatines which form the roof of the choanae and underlaps the presphenoid and the basisphenoid posteriorly. The pterygoid contacts the alisphenoid posteriorly and, anteriorly, has a very small contact with the maxilla posterolateral to the postpalatine foramen. The pterygoid of *Mayulestes ferox* is much larger that of the didelphids. It is very reduced in other borhyaenoids where it loses the hamular processes.

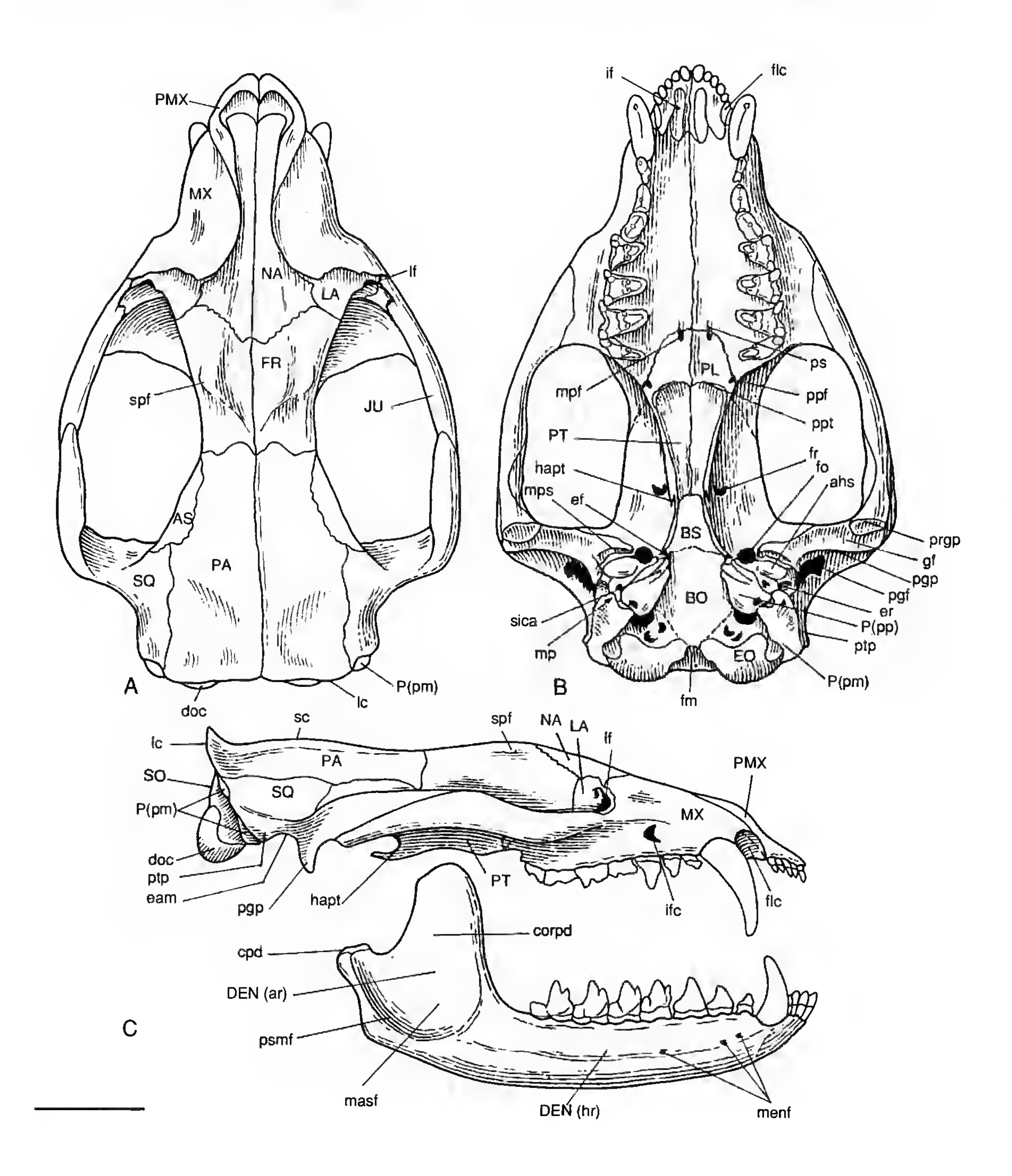
The choanal gutter of *Mayulestes* is very similar to that of didelphids: it is short anteroposteriorly and is bordered mostly by the pterygoids. In the other borhyaenoids the pterygoids are reduced and the choanal gutter is elongated. Its walls are formed by the sphenoidal processes of the palatines and the pterygoid processes of the alisphenoids. They are thick and their lateral side is buttressed by a salient ridge.

Lacrimal. (Figs 5, 6) The lacrimal forms the anterior border of the orbit. It has a large triangular portion on the dorsal surface of the skull. Its lateral portion is a small horn that articulates on the medial side of the anterior extremity of the jugal. The lacrimal articulates with the maxilla anteriorly, with the frontal posteromedially, with the nasal

FIG. 6. — *Mayulestes ferox*. Reconstruction of the skull and mandible (lateral view): **A**, dorsal; **B**, ventral; **C**, lateral views (the ascending ramus of the dentary, lacking in the holotype, has been reconstructed from the mandible of a recently discovered specimen probably referable to *Mayulestes*). Abbreviations: **AS**, alisphenoid; **ahs**, alisphenoid hypotympanic sinus; **BO**, basioccipital; **BS**, basisphenoid; **corpd**, coronoid process of dentary; **cpd**, condyloid process of dentary; **DEN(ar)**, ascending ramus of dentary; **DEN(hr)**, horizontal ramus of dentary; **doc**, dorsal occipital condyle; **eam**, external auditory meatus; **ef**, entocarotid foramen; **EO**, exoccipital; **er**, epitympanic recess; **flc**, fossa for lower canine; **fm**, foramen magnum; **fo**, foramen ovale; **FR**, frontal; **fr**, foramen rotundum; **gf**, glenoid fossa; **hapt**, hamular process of the pterygoid; **if**, incisive foramen; **ifc**, infraorbital canal; **JU**, jugal; **LA**, lacrimal; **lc**, lambdoidal crest (= nuchal crest); **lf**, lacrimal foramen; **mast**, masseteric fossa; **menf**, mental foramen; **mp**, mastoid process; **mpf**, medial palatine foramen, **mps**, medial process of the squamosal, **MX**, maxilla; **NA**, nasal; **PA**, parietal; **pgf**, postglenoid foramen; **pgp**, postglenoid process of the squamosal; **PL**, palatine; **PMX**, premaxilla; **P(pm)**, pars mastoidea of petromastoid (= mastoid *s.str.*); **P(pp)**, pars petrosa of petromastoid (= petrosal *s.str.*); **PT**, pterygoid; **ppf**, postpalatine foramen; **ppt**, postpalatine torus; **prgp**, preglenoid process of jugal; **ps**, palatine sulcus; **psmf**, posterior shelf of masseteric fossa; **ptp**, posttympanic process; **sc**, sagittal crest; **sica**, sulcus for the internal carotid artery; **SO**, supraoccipital; **spf**, supraorbital process of frontal; **SQ**, squamosal. Scale bar: 1 cm.

medially and with the jugal laterally. There are two lacrimal foramina. The medial foramen is large and wider than high. The lateral foramen is formed by two small superposed foramina.

Jugal. (Figs 5, 6) This bone is relatively long and slender when compared to what is observed in the other borhyaenoids. The anterior articulation with the maxilla is relatively short (30% of



the total length of the bone) and, in lateral view, it is less oblique than in the other borhyaenoids. The anteriormost extremity of the jugal is lateral to the anterior edge of M2. In ventral view, the jugal-maxilla suture is equidistant along all its length from the alveolar border and the sutures on both side of the specimen are slightly divergent posteriorly. Medially on its anterodorsal side, the jugal has a small articulation with the lacrimal. In lateral view, the bone is gently sigmoid. Its anterior portion is concave dorsally and forms the ventral border of the orbit. The transition from the orbit to the temporal fossa is hardly marked by the inflexion of the bone. The posterior portion of the bone is convex dorsally and is approximately 60% of the total length of the bone. At a level slightly anterior to the postorbital constriction, the jugal articulates dorsally with the zygomatic process of the squamosal. Its posterior extremity contributes to the anterolateral edge of the glenoid fossa. From the posterior end of the jugal-maxilla articulation to the anterior end of the jugal-squamosal articulation, the jugal has a constant width. It tapers rapidly towards its anterior extremity and gradually towards its posterior extremity. On the lateral side of the bone, a sigmoid rim and a shallow sulcus for the insertion of the masseter muscle run from the dorsal region of the posterior extremity to the ventral region of the jugal, at the level of the posterior extremity of the jugal-maxilla suture.

Frontal. (Figs 5, 6) In dorsal view, the frontals form the interorbital bridge located between the slightly longer rostrum and braincase. The frontals represent approximately 28% of the total length of the skull. Anteriorly they have a distinct W-shaped suture with the nasals and, on their anterolateral edge, a small suture with the lacrimals. The posterior suture with the parietals also has the shape of a W widely opened posteriorly. Lateral to the frontal-parietal suture, the dorsal part of the frontal-alisphenoid suture is subvertical; the ventral portion of the suture is not observable because of the crushing of the specimen. Very weak and rounded supraorbital processes (they resemble humps more than processes) are located dorsally in the middle of the lateral edge of the bone and a reduced interorbital constriction is located slightly anterior to the frontal-parietal suture. Supraorbital processes and interorbital constriction are much less developed than in the other borhyaenoids and the constriction is in a more posterior position than in the other borhyaenoids. In dorsal view, the frontals are much less opened anteriorly (*i.e.* the lateral edges of the bones are less diverging anteriorly) and much narrower posteriorly than in the other borhyaenoids. There is apparently no supraorbital foramen as in other borhyaenoids and in didelphids, although a tiny foramen below the right supraorbital "hump" could represent an actual supraorbital foramen.

On the lateral side of the skull, the relationships of the frontal with the palatine, the orbitosphenoid and the lacrimal are not observable because of the crushing of the skull.

Parietal and interparietal. (Figs 5, 6) The two bones are tightly fused and no suture can be distinguished between them. The bones are relatively flat which denotes small cerebral hemispheres. In the middle of each parietal, and medial to the anterior edge of the posterior root of the zygomatic arch, is a small prominence (corresponding to the cerebral hemispheres) and, located behind, a small depression just posterior to the anterior extremity of the bone. Behind the prominence is another depressed area which corresponds to the interparietal region anterior to the lambdoid crest. Except for the relatively weak (for a borhyaenoid) sagittal and lambdoid crests, the muscular attachment for the temporal muscle is not clearly evident as is observed in *Pucadelphys* by several irregular scars. Each parietal has a V-shaped suture with the frontal anteriorly (the V being wide open posteriorly), an oblique concave suture with the alisphenoid (*i.e.* the two parietal-alisphenoid sutures diverge posteriorly in dorsal view) and a concave, anteroposterioly oriented suture with the squamosal. The triple point between the parietal, the alisphenoid and the squamosal is located lateral to the hemispherical prominences of the parietal, approximately in the middle of the lateral edge of the parietal. Several small grooves or pits roughly aligned transversally are observed in the middle of the cranial vault, on both sides of the sagittal crest. They do not seem to correspond to muscu-

lar attachments but probably represent scars due to injuries resulting from the attack of a predator on the head of the holotype of *Mayulestes ferox*, catching it from above and to the side.

Orbitosphenoid. (Figs 5, 6) This bone is preserved but it is badly crushed. It can be observed in the bottom of the large optic-orbital foramen. The lateral wall of this foramen is formed by the alisphenoid and the medial wall is formed by the orbitosphenoid. The foramen is located dorsolateral to the base of the hamular process of the pterygoid. In the specimen described here, a portion of the alisphenoid artificially overlaps the anteromedial edge of the optic-orbital foramen. Approximately 5 mm beyond the posterolateral rim of the optic-orbital foramen, at the suture between the orbitosphenoid and the frontal is the ethmoidal foramen, which is located dorsolaterally to the anterior third of the pterygoid. The optic-orbital foramen and the ethmoid foramen are located in a slightly more posterior position than in the living *Didelphis*. The optic-orbital foramen transmits the cranial nerves II, III, IV, V1, VI, the ophtalmic artery and a vein which drains the eye to the cavernous sinus. The ethmoid foramen transmits a branch of the internal carotid from the orbit into the olfactory region of the cranial cavity (Archer 1976).

Alisphenoid. (Figs 5C, 6C, 7, 8) This bone forms the anteroventrolateral region of the braincase. It has a large articulation with the frontal anteriorly and laterally; with the parietal dorsolaterally and with the squamosal posterolaterally. The alisphenoid articulates with the orbitosphenoid medially, the palatine and the pterygoid anteriorly and the basisphenoid and the periotic posteriorly. Anteromedially, the alisphenoid forms the posterior rim of the optic-orbital foramen. Postero-lateral to it is a large foramen rotundum (which transmits the maxillary branch of the trigeminal nerve, V2) which opens anteriorly. Lateral to the foramen rotundum is a wide groove bordered laterally by a sharp crest, obliquely oriented (*i.e.* in anteromedial-posterolateral direction). This structure represents the ventralmost extension of the origin of the temporalis muscle, which was apparently well-developed in *Mayulestes*. This structure is also observed in *Didelphis*, although here it is much less pronounced. It is absent in *Borhyaena*, *Cladosictis* and *Sipalocyon*, but it is very well-developed in *Prothylacynus* where strong fossae, grooves and crests are present in that region of the skull. Posteromedial to the foramen rotundum, the alisphenoid borders the basisphenoid laterally and, at the posterolateral extremity of this bone, it contributes to the formation of the dorsal wall of the entocarotid foramen (which transmits the internal carotid artery and a small vein from the inferior petrosal sinus). Lateral to the entocarotid foramen, the alisphenoid forms the anterior edge of the foramen ovale and the foramen lacerum medium. Because of the deformation of the skull it is not certain whether the foramen ovale and the foramen laccrum medium were separated from each other by a bony wall or were confluent, although the first interpretation is more probable. Posterolaterally, the alisphenoid contributes to the formation of the alisphenoid hypotympanic sinus (see Muizon 1994) where it is wedged between the petiotic posteromedially and the medial process of the squamosal anterolaterally. The alisphenoid does not possess any tympanic process, not even incipient. No transverse canal is observed lateral to the suture with the basioccipital. Laterally, the alisphenoid contributes to the formation of the anteromedial angle of the glenoid fossa.

Basisphenoid. (Figs 5C, 6C, 7, 8) It is a large trapezoid bone narrow anteriorly and wide posteriorly. It is anteriorly underlapped by the sphenoid processes of the pterygoids which hide its suture with the presphenoid. The bone is bordered by two lateral crests which are higher in their anterior portion. Along these crests, the basisphenoid is tightly articulated with the alisphenoid but the suture is clearly visible on both sides of the specimen. On the posterolateral angle, a reasonably developed entocarotid foramen opens wherein the ventromedial edge is formed by the basisphenoid. The bone is flat on most of its surface, except for the lateral crests and a small median ridge that occurs in its anterior region and which tapers rapidly posteriorly. The suture with the basioccipital is straight, transverse and joins the anterior extremity of the periotics.

Squamosal. (Figs 5-8) Dorsally, the squamosal

articulates with the posterior lateral half of the parietal in a convex suture. Anterolaterally, it has a subvertical suture with the alisphenoid which turns laterally and passes on the ventral side of the skull, where it cuts obliquely the anteromedial angle of the glenoid fossa. It then runs medially, almost reaching the lateral border of the foramen ovale. In this area the squamosal possesses a medial indentation [called here the medial process of the squamosal (Muizon 1994)] which is also present in the other borhyaenoids, and in Andino-delphys *Pucadelphys* but absent in other marsupials (see discussion below). The posterior edge of this process is excavated by the roof of the alisphenoid hypotympanic sinus and its ventral side bears a conspicuous ridge which almost joins the medial edge of the glenoid fossa to the lateral border of the foramen ovale (the anterior crest of the alisphenoid hypotympanic sinus; Fig. 7). The medial process of the squamosal articulates with the alisphenoid and, at the point where the suture leaves the alisphenoid hypotympanic sinus posteriorly, the squamosal articulates with the periotic. The suture runs along the lateral border of the epitympanic recess and the fossa incudis. Further posteriorly, the squamosal has an irregular contact with the lateral surface of the pars mastoidea of the periotic. The periotic-squamosal suture is visible in dorsal view of the skull where a small portion of the pars mastoidea is not covered by the squamosal and is part of the lambdoid crest.

The glenoid fossa is deep and elongated transversely. In this respect it resembles that of *Borhyaena*, more than that of any other borhyaenoid. The axes of the glenoid fossae are not exactly parallel as in *Borhyaena* and *Prothylacynus* but are slightly oblique in relation to the anteroposterior axis of the skull. Its anteromedial angle is formed by a small contribution of the alisphenoid as observed in most didelphids and peramelids, contrary to the other borhyaenoids. The postglenoid process is very wide and high. It has a rounded outline and is approximately symmetrical in posterior view (*i.e.* its greatest ventral expansion is located at the middle of the glenoid fossa). The preglenoid process of the jugal is much smaller and is located at the anterolateral angle of the glenoid fossa. The postglenoid foramen is located on the posteromedial edge of the postglenoid process. The vessels it transmits continue their course in a groove along the ventromedial edge of the postglenoid process. The groove disappears approximately in the middle of the ventral edge of the process. The postglenoid foramen is exclusively formed by the squamosal, while internally the medial wall of the canal is formed by the lateral side of the periotic and the medial wall is formed by the squamosal. The postglenoid foramen transmits the sphenoparietal emissary vein (which externally becomes the postglenoid vein) from the prootic sinus (Wible 1990) and the postglenoid artery (Archer 1976; Wible 1990).

The subsquamosal foramen is preserved on the left side of the specimen but it is reduced to a small slit (probably slightly flattened by the deformation of the skull) posterodorsal to the postglenoid foramen, just dorsal to the external acoustic meatus. It differs from what is observed in all other borhyaenoids where the subsquamosal foramen is always much larger, but clearly resembles that of the stagodontid *Eodelphis cutleri* from the Late Cretaceous of Canada. The subsquamosal foramen opens into the postglenoid foramen and transmits an artery from the postglenoid foramen onto the parietal area of the cranium, which supplies the temporalis muscle, and a vein from the sphenoparietal emissary vein, which exits through the postglenoid foramen (Archer 1976; Wible 1990).

There are no obvious postzygomatic foramina, contrary to the condition observed in *Pucadelphys*. However, the small foramen located in the groove of the postglenoid foramen could represent the postzygomatic foramen which migrated medially from its position dorsomedial to the apex of the glenoid process. The condition of *Mayulestes* is found in the other borhyaenoids and in *Didelphis*. The postzygomatic foramen transmits a vein from the posterior root of the zygomatic arch to the sphenoparietal emissary vein (Archer 1976). In some other Borhyaenoidea (*Prothylacynus*, *Cladosictis*, *Sipalocyon* and *Sallacyon*) another foramen is present on the lateral face of the zygomatic process of the squamosal, just above the glenoid fossa. In didelphids, when present, this foramen is connected

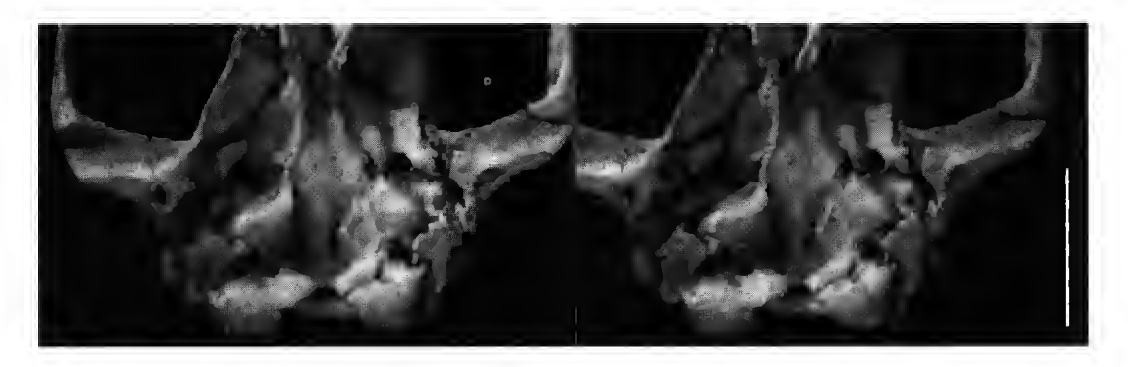


FIG. 7. — *Mayulestes ferox*, holotype (MHNC 1249). Basicranium. Scale bar: 1 cm.

to the postzygomatic foramen. The same is probably true in borhyaenoids although the second foramen is located further anteriorly than in didelphids and therefore more distant from the postzygomatic foramen.

Because the pars mastoidea of the periotic has been displaced from its original contact with the squamosal, it is difficult to observe the posttemporal foramen. However, the pars mastoidea of the right periotic shows a clear small notch on its ventrolateral angle which could represent the posttemporal foramen. If this interpretation is correct, the foramen would be in a much lower position than in *Didelphis* and *Pucadelphys*. The posttympanic foramen carries the arteria diploetica magna and the vena diploetica magna which pass through a canal bordered by the periotic medially and the squamosal laterally (Wible 1990).

Periotic. (Figs 7, 8) This bone includes two components: the pars mastoidea which largely contributes to the formation of the lateral part of the occipital view and houses the subarcuate fossa on the cerebellar side; and the pars petrosa which houses the inner ear, semicircular canals and cochlea in the promontorium, and, on the cerebellar surface, the internal auditory meatus.

The large pars mastoidea of *Mayulestes* forms the lateral area of the occipital shield. It differs from that of all the other borhyaenoids where it is totally internal and does not outcrop on the posterior face of the skull. In *Mayulestes*, it is wedged between the exoccipital ventromedially, the supraoccipital dorsomedially and the squamosal anteriorly. A small mastoid foramen is present on the dorsomedial region of the occipital side of the pars mastoidea, just lateral to its suture with the supraoccipital. In posterior view, the pars mastoidea has a reniform shape with a concave medial edge and a lateral edge straight in its middle and more or less convex at its extremities. The surface of the pars mastoidea is mostly flat, but concave in the area of the mastoid foramen. The anteroventral edge of the pars mastoidea is formed by the caudal tympanic process of the periotic (*sensu* Wible 1990). Its ventrolateral extremity bears a small and rounded mastoid process but is relatively salient ventrally and posteriorly. Dorsolateral to the mastoid process is a small rim which is bordered laterally by the squamosal. In the middle of that ridge is a foramen of reasonable size which has not been found in other Recent or living marsupials. Its function has not been elucidated. Anterodorsally to the mastoid process is a small saddle-shaped groove for the passage of the facial nerve: the stylomastoid notch.

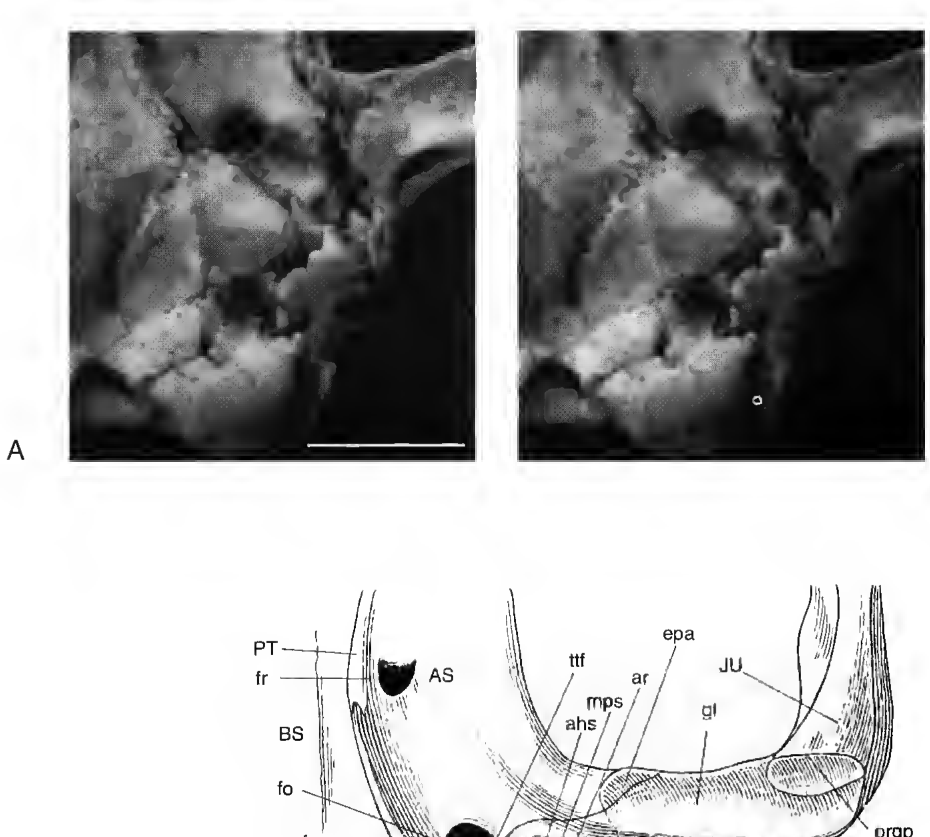
The ventral or tympanic side of the periotic is formed by the large teardrop-shaped promontorium which represents the pars cochlearis, and by the portion of the periotic posterior and lateral to the promontorium, the pars canalicularis. The posterior region of the promontorium is the thickest and bears a small tubercle just ventral to the cochlear window. A similar tubercle is also observed in *Sipalocyon*. This morphology has been noted by Archer (1976: 291) who observed on the right promontorium of AMNH 9254 (*Sipalocyon gracilis*) a transverse swelling posterior to a small depression that he regards as homologous to the tympanic wing of the petro-

sal in other marsupicarnivores. In *Mayulestes* the tubercle is exactly in the same position as the rostral tympanic process of the periotic [= tympanic wing of the petrosal of Archer (1976)] observed in living didelphids. From that tubercle a shallow depression runs anteromedially, turns anteriorly and becomes a deep groove at the apex of the promontorium. This sulcus marks the route of passage of the internal carotid artery, which enters the skull *via* the entocarotid foramen located anteromedial to the foramen ovale, and is formed by the alisphenoid dorsolaterally and the basisphenoid ventromedially. The passage of the internal carotid is thus situated medially (*sensu* Presley 1979). Lateral to the sulcus for the internal carotid artery is a large fossa on the lateral side of the promontorium for the insertion of the stapedial muscle. This fossa is separated from the sulcus for the internal carotid by a high, bony wall. The medial side of the promontorium has a sigmoid outline: it is deeply concave in its posterior region (medial to the tubercle mentioned above) and largely convex in its anterior part forming a blade-like expansion which articulates with the basioccipital. The medial border of the promontorium is the ventral border of a deep medial sulcus for the passage of the inferior petrosal sinus. This vessel is a vein which connects the cavernous sinus (encasing the pituitary gland and the optic chiasma) with the jugular vein just before it emerges from the inferior petrosal foramen (MacIntyre 1972: 291). The sulcus for the jugular vein was misidentified as a sulcus for a branch of the internal carotid artery by Patterson (1965), Clemens (1966) and Marshall (1977a, 1978). The concave edge of the posteromedial border of the promontorium corresponds to the dorsolateral rim of the inferior petrosal foramen.

Two openings exist on the posterior region of the promontorium: the fenestra cochleae and the fenestra vestibuli. The fenestra cochleae is situated on the posterolateral surface of the promontorium, just medial to the stylomastoid notch. It has an ovoid shape with its ventral rim more convex than the dorsal as observed in *Pucadelphys* and other borhyaenoids. The fossula fenestra cochleae, which is well marked in *Pucadelphys* and in the Late Cretaceous petrosal type A, B and C of Wible (1990), is absent in *Mayulestes* as in the other borhyaenoids. Posteromediodorsal to the fenestra cochleae is a funnel-shaped pit opening posterolaterally, which houses the opening of the aqueductus cochleae which opens in the posterior lacerate foramen. The anterolateral rim of the posterior lacerate foramen is formed by the periotic and its posteromedial rim formed by the exoccipital. On the anterolateral side of the promontorium is the fenestra vestibuli which is hardly visible (as it is reduced to a simple slit) because of the dorsoventral squeezing of the specimen. Its posterior end is located just medial to the bony trabecula that makes the junction between the pars mastoidea and the pars petrosa: the crista parotica. On the right periotic it is possible to observe that the fenestra vestibuli is located within a shallow depression, the fossula fenestra vestibuli.

Laterally, the promontorium is bordered by a deep, L-shaped groove, which passes between the promontorium and the epitympanic recess anteriorly and between the promontorium and the caudal tympanic process of the periotic, posteriorly. The posteromedial extremity of the groove is formed by the anterolateral wall of the posterior lacerate foramen. The cavity located lateral to this wall, posterior to the posterior border of the promontorium and anterior to the caudal tympanic process of the periotic, is the mastoid epitympanic sinus. Anterolateral to this sinus and lateral to the fenestra vestibuli is a shallow cupule which receives the origin of the stapedius muscle: the fossa stapedius. The stylomastoid notch forms the angle of the L and ventral to it and lateral to the stapedius fossa is the crista parotica, which separates the fossa stapedius medially and the fossa incudis laterally.

Anterior to the fossa incudis is the epitympanic recess. This structure has been defined by Van der Klaauw (1931: 73) and Archer (1976a: 226) and a clear and simple definition has been given by Wible (1990: 188): it is "[...] the extension of the middle ear cavity that lies dorsal to the tympanic membrane and contains the mallear-incudal articulation". In *Didelphis* the epitympanic recess is a small elongated fossa located dorsomedial to the dorsal rim of the external auditory meatus, ventral to the prootic canal and lateral



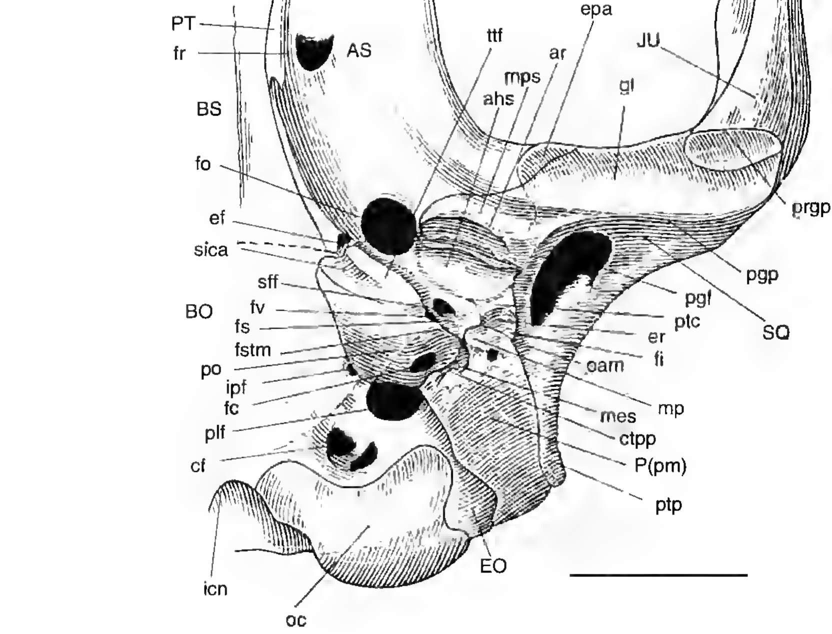


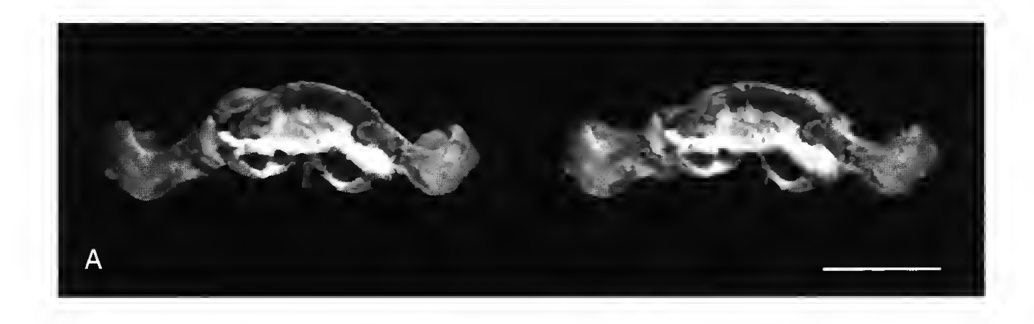
Fig. 8. — *Mayulestes ferox*, left ear region: **A**, holotype (MHNC 1249); **B**, reconstruction. Abbreviations: **ahs**, alisphenoid hypotympanic sinus; **ar**, anterior ridge of the alisphenoid hypotympanic sinus; **AS**, alisphenoid; **BO**, basioccipital; **BS**, basisphenoid; **cf**, condyloid foramen; **ctpp**, caudal tympanic process of pars mastoidea of petromastoid; **eam**, external auditory meatus; **ef**, entocarotid foramen; **EO**, exoccipital; **epa**, entoglenoid process of the alisphenoid; **er**, epitympanic recess; **fc**, fenestra cochleae; **fi**, fossa incudis; **fo**, foramen ovale; **fr**, foramen rotundum; **fs**, facial sulcus; **fstm**, fossa for stapedial muscle; **fv**, fenestra vestibuli; **gf**, glenoid fossa; **icn**, intercondylar notch; **ipf**, inferior petrosal foramen; **JU**, jugal; **mes**, mastoid epitympanic sinus; **mp**, mastoid process; **mps**, medial process of the squamosal; **oc**, occipital condyle; **pgf**, postglenoid foramen; **plf**, posterior lacerate foramen; **P(pm)**, pars mastoidea of periotic; **pgp**, postglenoid process of squamosal; **po**, promontorium of pars petrosa of petromastoid; **prgp**, preglenoid process of the jugal; **PT**, pterygoid; **ptc**, petrosal crest; **ptp**, posttympanic process; **sff**, secondary facial foramen; **sica**, sulcus for internal carotid artery; **SQ**, squamosal; **ttf**, tensor tympani fossa. Scale bars: 5 mm.

and parallel to a line joining the secondary facial foramen and the fenestra vestibuli. It is limited laterally by the dorsal rim of the external auditory meatus of the squamosal and anteriorly by an elevated oblique (anterolateral-posteromedial) ridge called the petrosal crest. In living didelphids, the petrosal crest joins the triple point periotic-squamosal-alisphenoid (laterally) and a small crest [roughly anteroposteriorly oriented (precisely, anteromedial-posterolateral)] flooring the medial opening of the prootic canal (medially). The petrosal crest also delineates the posterolateral border of the alisphenoid sinus which is excavated in the periotic in its posterior portion. The rest of the alisphenoid hypotympanic (in didelphids the sinus is actually, at least in part, hypotympanic) sinus (*i.e.* most of it) is excavated in the alisphenoid. The posterior region of the alisphenoid in the sinus underlaps a small portion of the periotic. The posterior portion of the alisphenoid hypotympanic sinus, the anterior portion of the epitympanic recess and the ridge that separates them, form, in the periotic, a small ventrally directed triedra that Wible (1990, fig. 4) termed the lateral wall of the epitympanic recess. Consequently, the fossa anterior to the petrosal crest, in Wible's illustrations (1990, figs 2F, 4C), do not represent part of the epitympanic recess but the periotic portion of the alisphenoid hypotympanic sinus. As it will be shown below, the so-called alisphenoid hypotympanic sinus is not always excavated mainly in the alisphenoid and is not always hypotympanic [a contradiction also noted by Archer (1976a: 127)]. However, since the morphology of the middle ear sinus of *Mayulestes* is regarded here as homologous to that of the other borhyaenoids and although the term hypotympanic is inappropriate in the case of *Mayulestes*, it will be used here (as elsewhere, Muizon 1994) in order to avoid confusion.

In *Mayulestes*, the epitympanic recess is an elongated fossa limited posteriorly by the dorsal portion of the crista parotica and anteriorly by the petrosal crest. The small pit at its posterolateral extremity, lateral to the dorsal part of the crista parotica, is the fossa incudis (or fossa crus breve incudis) where the ligament of the small process of the incus is attached. The epitympanic recess and the fossa incudis are bordered laterally by the dorsal rim of the external auditory meatus of the squamosal. However, because of the crushing of the specimen described here, they are opened laterally since their lateral wall is displaced laterally. Following Wible (1989, fig. 4A, C), Muizon (1994, fig. 2a) misidentified the epitympanic recess of *Mayulestes*. What I identified as the epitympanic recess is in fact the posterior part of the alisphenoid hypotympanic sinus and the fossa incudis (*in* Muizon 1994) is the epitymapnic recess. In its anterior portion, the epitympanic recess is bordered by two small crests. The lateral one was probably in contact with the squamosal or close to it and is medial to the ventral opening of the sulcus for the prootic sinus. The medial crest forms the floor of a small trough located just lateral to the secondary facial foramen and dorsolateral to the petrosal crest. This trough, in didelphids, houses the medial opening of the prootic canal. In *Mayulestes* the prootic canal is absent. On the lateral side of the right periotic, the sulcus for the prootic sinus is clearly visible because of the opening of the squamosal-periotic suture due to the crushing of the skull. Peering through the sinus, it is not possible to observe any lateral foramen of the prootic canal. Medial to the medial extremity of the petrosal crest is the secondary facial foramen which opens posteriorly and through which is passing the facial nerve.

Beyond the petrosal crest is a large (but small for a borhyaenoid) alisphenoid hypotympanic sinus. It is made of three different bones, the periotic, the alisphenoid and the squamosal. Its posterior half is excavated in the periotic. In *Mayulestes* it is approximately half of the sinus while in *Didelphis* that region of the periotic is totally covered by the alisphenoid ventrally. The anterolateral half of the sinus is formed by a small strip of the alisphenoid, posteromedially, and by the posterior wall of the medial process of the squamosal, anterolaterally. The alisphenoid-squamosal suture has a distinct sigmoid morphology. The anterior border of the alisphenoid sinus is formed by the medial process of the squamosal which bears a conspicuous ridge (the anterior ridge of the alisphenoid hypotympanic sinus) which almost joins the medial border of the gle-

noid fossa to the lateral border of the foramen ovale.
Anteriorly, between the fossa for the tensor tympani muscle and its lateral border, the periotic forms the posterior border of the foramen ovale. This condition is primitive for marsupials (Muizon *et al.* 1997) and will be discussed below.
Ectotympanic. No ectotympanic has been found with the type specimen of *Mayulestes*. In other borhyaenoids, the ectotympanic articulates with the squamosal between the medial edges of the postglenoid process and postglenoid foramen and the medial process of the squamosal. The alisphenoid also participates in the articulation and small contact may exist with the posttympanic process of the squamosal posteroventrally. A shallow groove and small ridges can be observed in this area and evidences the articulation with the ectotympanic. In *Mayulestes* this region of the skull is damaged on both sides of the specimen. However, on the right side of the skull, it is possible to observe the contact between the squamosal, medial to the postglenoid foramen, and the periotic, lateral to the lateral extremity of the petrosal crest and the periotic part of the hypotympanic sinus. A fairly good reconstruction of this region of the skull is possible, and apparently, there was no groove or ridge for the articulation of the ectotympanic, although very subtle undulations of the squamosal in this area are observable with incident light. Therefore, it seems that the ectotympanic of *Mayulestes* was not tightly imbricated with the squamosal as in other borhyaenoids. This bone was probably maintained in its position by ligaments only, but perhaps appressed against the squamosal in a position that could represent an incipient development of the condition observed in the other borhyaenoids. This condition seems to be intermediate between that of *Didelphis* – where the ectotympanic is attached to the alisphenoid by ligaments only, and has no true articulation with the skull – and that of other borhyaenoids.
Basioccipital. (Figs 5C, 6C, 7) Because of the dorsoventral crushing of the skull, the bone has been pushed dorsally within the braincase and occupies a position dorsal to the periotics wherein the inferior petrosal sinus is exposed medially. The basioccipital is a short, broad, trapezoidal bone which contrasts with that of the other borhyaenoids where it is generally longer and narrower. In this respect, it is more similar to that observed in *Didelphis*. The basioccipital has a broad, transverse suture with the basisphenoid anteriorly. Posterolaterally, at its contact with the periotic, the basioccipital is inflated, a morphology which indicates the passage of the inferior petrosal sinus. Its articulation with the exoccipital is formed by two oblique lines which join the posteromedial angle of the promontoria to the central region of the ventral rim of the foramen magnum which is formed by the basioccipital. The bone has a small median keel which starts at the basisphenoid-basioccipital suture and which affects the anterior two thirds of the bone. On each side of this keel are two deep fossae for the origin of the rectus capitis ventralis muscle.
Exoccipital. (Fig. 9) This bone contacts the periotic medially and forms the posterodorsal wall of the inferior petrosal foramen, and the medial and posterior rim of the foramen lacerum posterior (which transmits the nerves IX, X, XI, and probably a small branch of the sigmoid sinus, to the internal jugular vein). Anteriorly it has a small contact with the pars petrosa of the periotic by the septum between the inferior petrosal and posterior lacerate foramina and laterally it contacts the pars mastoidea of the periotic.
On the ventral side of the exoccipital, anterior to the ventral portion of the occipital condyle, are two condyloid foramina which probably transmitted branches of the nerve XII (Jollie 1962) but may also carry branches of the sigmoid sinus to the internal jugular vein (Archer 1976).
In posterior view, because of the crushing of the skull, the foramen magnum is flattened dorsoventrally and the occipital condyles are "folded" and broken. It is however possible to note that the exoccipitals had a large, convex suture with the pars mastoidea of the periotic (*i.e.* the lateral edge of the exoccipital is convex). The suture with the supraoccipital is slightly convex (*i.e.* the dorsal edge of the exoccipital is convex) and runs from the dorsomedial region of the mastoid process to the dorsal rim of the foramen magnum. The paroccipital process, if present, was very small. The occipital condyles are very large but much less salient than in the other borhyaenoids.



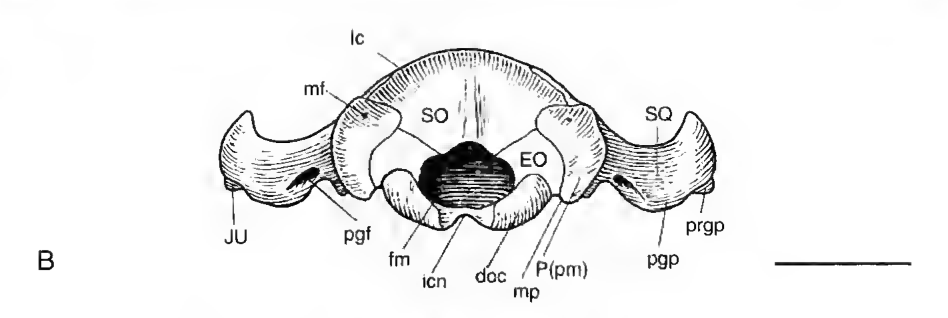


Fig. 9. — *Mayulestes ferox*, skull in occipital view: **A**, holotype, (MHNC 1249) ; **B**, reconstruction. Abbreviations: **EO**, exoccipital; **fm**, foramen magnum; **icn**, intercondylar notch; **JU**, jugal; **lc**, lambdoidal crest; **mf**, mastoid foramen; **mp**, mastoid process; **doc**, dorsal occipital condyle; **P(pm)**, pars mastoidea of the periotic; **pgf**, postglenoid foramen; **pgp**, postglenoid process of the squamosal; **prgp**, preglenoid process of the jugal; **SO**, supraoccipital; **SQ**, squamosal. Scale bars: 1 cm.

In this respect they are more similar to those of *Didelphis*. On the dorsal rim of the foramen magnum, the exoccipitals are broadly separated as observed in *Pucadelphys*, contrary to the condition of *Didelphis*. The condition in the other borhyaenoids was difficult to evaluate as in all the specimens available during this study the exoccipitals were tightly fused to the supraoccipital.

Supraoccipital. (Fig. 9) This bone occupies the dorsal central area of the occipital shield and forms an important portion of the dorsal rim of the foramen magnum. The bone articulates ventrolaterally with the exoccipital, laterally with the pars mastoidea of the periotic and dorsally with the postparietal. Apparently, the suture with the postparietal is located on the lambdoidal crest itself. The surface of the supraoccipital is relatively smooth. However, the posteriorly protruding lambdoidal crest forms a very deep fossa for the attachment of the nuchal muscles. Several small foramina are present, mainly at the base of the lambdoid crest.

Dentary (Fig. 3)

The dentary of *Mayulestes* is known by its horizontal ramus and fragments of the condyle and angular process. The proportions of the horizontal ramus compare favourably with *Cladosictis*. It is relatively high compared to didelphids and *Sipalocyon* and is more slender than in *Prothylacynus* and *Borhyaena*. The anterior part of the ramus (below the incisors, canine and p1) has a relatively straight ventral border which makes an angle of approximately 45° with the axis of the tooth row. Below p2 and p3 the ventral border of the ramus is slightly concave and gently convex below the molars. This morphology is similar to that observed in *Cladosictis centralis* and *Sipalocyon gracilis* although less emphasised in these species than in *Mayulestes ferox*. Two large mental foramina occur below the anterior root of p2 and the middle of m1. A much smaller foramen is located below the posterior root of p2. Medially, the articular surface of the symphysis is similar in shape to that of *Sipalocyon* and *Cladosictis* but slightly shorter

anteroposteriorly. Its posterior extremity is situated below the posterior root of p2 while in the former two genera it is below the anterior root of p3 (it is sometimes below p2 in *Sipalocyon*). The articular surface is less rugose than in *Sipalocyon* and *Cladosictis*. As in those genera, the articular surface is roughly parallel to the plane of the horizontal ramus below the molars while in didelphids it is at an angle of approximately 20°. The mylohyoid groove is well marked and ends anteriorly below m1.

POSTCRANIAL SKELETON

Atlas (Fig. 10)

The atlas lacks the ventral arch (the intercentrum of the atlas) which was not fused to the rest of the vertebra and was lost prior to fossilization. The dorsal arch is long anteroposteriorly in its dorsomedial part (5.5 mm) and short ventrolaterally, above the transverse process (3.2 mm). In this respect, the dorsal arch of the atlas of *Mayulestes* resembles more that of *Borhyaena* than those of *Cladosictis*, *Sipalocyon* and *Prothylacynus*. This condition is also present in *Pucadelphys* (Marshall & Sigogneau-Russell 1995) but less marked. The dorsal arch of the atlas of *Mayulestes* has strongly convex anterior and posterior edges and the anterior is clearly recurved ventrally in its median region. Strongly convex anterior and posterior borders of the dorsal arch are also found in *Borhyaena* while it is either straight or concave in *Prothylacynus*, *Cladosictis*, *Sipalocyon*, *Didelphis* and *Thylacinus*. In *Borhyaena*, however, the anterior border of the arch is not recurved ventrally. The dorsal arch of *Mayulestes* is wide transversally and the neural canal is almost twice as wide than high as observed in *Didelphis*. It differs in this respect from the other borhyaenoids where the dorsal arch is shorter transversally and where the neural canal is only slightly wider than high. This condition is unknown in *Pucadelphys*. On the lateral extremities of the anterior and posterior edges of the dorsal arch there are deep grooves (the posterior grooves are deeper than the anterior grooves) for the passage of the first cervical nerve and the vertebral artery anteriorly, and a ramification of the latter posteriorly. The condition of *Mayulestes* is different from that of all the other borhyaenoids for which the atlas is known. In *Borhyaena* the anterior groove is present but the posterior is lacking. In *Prothylacynus*, *Cladosictis* and *Sipalocyon*, the anterior sulcus is closed in an intervertebral foramen (or atlantal foramen) and the posterior is absent. The absence of the posterior sulcus in the Santa Cruz borhyaenoids is probably a consequence of the presence of a small transverse foramen, a structure absent in *Mayulestes*. An intervertebral foramen is also found in *Didelphis* and *Thylacinus* but is absent in *Marmosa*, *Perameles* and *Monodelphis*. The condition observed in *Mayulestes* is similar to that observed in *Pucadelphys*, a Palaeocene didelphoid which has neither intervertebral nor transverse foramina (Marshall & Sigogneau-Russell 1995).

The transverse processes or wings of the atlas are partially broken in the specimen described here, but it is clear that they were smaller than those of the other borhyaenoids. In *Mayulestes* the processes are strongly constricted at their bases because of the depth of the arterial grooves. On the ventral border of the right transverse process (which is better preserved than the left one), at its base, is an anteroposterior groove which was transmitting the vertebral artery posteriorly to the axis.

The anterior articular facets with the occipital condyles are more opened anteriorly (*i.e.* they are facing more anteriorly than medially) than in the other borhyaenoids where they are facing more medially than anteriorly. This condition is also found in *Didelphis* and *Thylacinus*. The posterior articular facets with the axis are simply reniform and similar to those of *Didelphis*. They are much less concave than the occipital facets.

Axis (Fig. 11)

The most spectacular feature of the axis is the size of its extremely long, triangular-shaped spinous process. It is fairly similar to those of *Borhyaena*, *Prothylacynus* and *Cladosictis* but clearly differs from the highly specialised process of *Didelphis* (*Didelphis* has cervical vertebrae 2 to 5 with transversely thickened spinous processes which tend to synostose with each other). It is much longer anteroposteriorly than in *Pucadelphys* and any other didelphid. The dorsal edge of the spinous process of the axis of

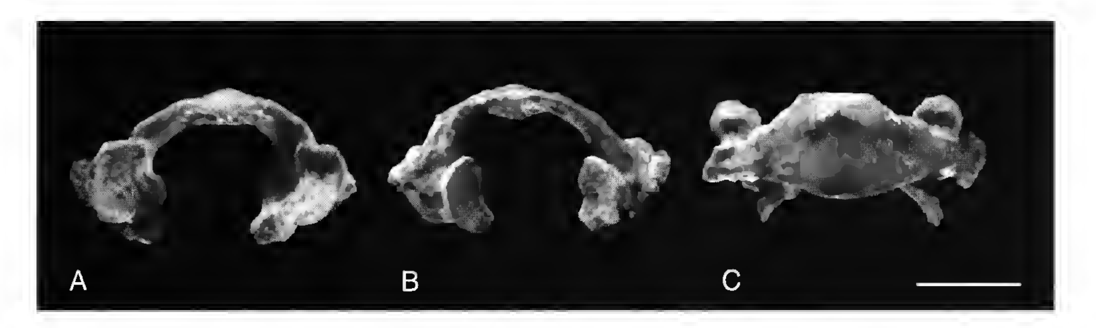


FIG. 10. — *Mayulestes ferox*, holotype (MHNC 1249). Atlas: **A**, anterior; **B**, dorsal; **C**, posterior views. Scale bar: 5 mm.

Mayulestes is very convex anteriorly and almost straight in its posterior two thirds. The posteroventral edge is straight and oblique and forms an angle close to 35° with the dorsal edge. The anteroventral edge is regularly concave and passes to the anterior border of the pedicles of the neural arch which contact the body of the axis in a point more posterior than in other borhyaenoids. Anteroposteriorly, the pedicles are proportionally shorter and the whole neural arch is located in a more posterior position than in *Borhyaena*, *Prothylacynus* and *Cladosictis*: in dorsal view the visible portion of the anterior part of the body (mainly the portion corresponding to the centrum of the atlas) is larger, and in ventral view the visible portion of the neural arch is also larger. The postzygapophysial facets are more widely separated than in *Borhyaena* and the neural canal is proportionally much larger. Ventrally to the postzygapophyses, the transverse processes are divided into a large dorsal portion and a small ventral ridge. As a consequence, the transverse foramen is opened laterally and the dorsal transverse processes overhang an elongated fossa (transverse sulcus) for the passage of the vertebral artery. As in *Pucadelphys*, there is no transverse foramen, contrary to the condition of *Borhyaena*, *Prothylacynus*, *Cladosictis*, *Didelphis* and *Thylacinus*.

The atlantal and axial component of the axis are coossified and their suture is observable on the ventral surface of the vertebra as an elevated transverse ridge. The centrum of the vertebra (composed of the centrum of the atlas, anteriorly, fused to the centrum of the axis, posteriorly) is wide and relatively shorter than in the other borhyaenoids. Anteriorly, it bears a small odontoid process between the two anterior articular facets for the atlas, all three similar in proportions to those of *Borhyaena*. On the ventral face of the centrum are two deep fossae for the attachment of the longus colli muscle, an important depressor of the head. The fossae occupy the total width of the body posteriorly and slightly narrow anteriorly, where the body is wider because of the anterior articular facets (the body of the atlas). The apices of the fossae are rounded and almost reach the base of the odontoid process. The fossae for the longus colli are more developed than in *Borhyaena*, where they are triangular and narrow anteriorly, and in *Prothylacynus*, where they do not reach the base of the odontoid process. The longus colli fossae are separated by a sharp median crest concave in lateral view and forming a small posterior tubercle projecting ventrally. The median crest and tubercle of *Mayulestes* are less developed and project less ventrally than in other borhyaenoids, which could indicate a slightly weaker musculature. The fossae are bordered anterolaterally by two crests for the attachment of the longus capitis muscle, another depressor of the head. Since there is no transverse foramen in *Mayulestes*, these crests do not extend laterally on the ventral edge of the transverse process ventrally (therefore ventrally to the vertebral artery), as it is observed in *Borhyaena*, *Prothylacynus*, *Cladosictis*, and *Thylacinus*. In *Mayulestes* the origin of the longus capitis was probably restricted to the anterolateral region of the ventral face of the centrum.

In posterior view, the centrum is much lower than in *Borhyaena*, *Prothylacynus*, *Cladosictis* and



Fig. 11. — *Mayulestes ferox*, holotype (MHNC 1249). Axis: **A**, lateral; **B**, dorsal views. Scale bar: 5 mm.

Thylacinus but shows a condition similar to that of *Didelphis*. The articular surface for the third cervical vertebra faces posterodorsally.

Other cervical vertebrae

Two other partial cervical vertebrae are known (the ?third and the ?fifth). The ?third cervical vertebra is only known by its centrum, which is very low and short like that of the axis. The ?fifth cervical vertebra is better preserved but is missing most of the neural arch. The centrum is proportionally shorter than in the Santa Cruz borhyaenoids. Its ventral surface has a weakly developed relief, being excavated ventrally by two shallow fossae for the longus colli muscles. It clearly differs from the cervical vertebrae of *Prothylacynus* and *Borhyaena* which bear a very strong ventral crest with a large posterior tubercle (extremely thick in YPM PU 15120). Dorsally, the centrum presents two deep excavations probably related to the passage of the ventral spinal artery and its ramifications to the vertebral artery. At the base of the transverse process is a relatively large transverse foramen for the passage of the vertebral artery. The pedicle of the neural arch is short.

Thoracic vertebrae (Fig. 12)

Five thoracic vertebrae are known, three anterior and two posterior. Of the three anterior vertebrae only one is complete. It is referable to T1 or T2 since the prezygapophyses are facing dorsomedially and the postzygapophyses are facing ventrally (tangential). This condition is observed on T1 in *Caluromys*, *Didelphis* and *Phalanger*, but on T2 in *Monodelphis* and *Metachirus*. Since the first three genera are arboreal and the last two are terrestrial and, given the interpretation given below of the mode of life of *Mayulestes* (at least partially arboreal), it is more likely that this vertebra represents the T1. Its neural arch is very wide and the prezygapophyses are greatly separated. The articular facets face dorsomedially and not dorsally as in the more posterior vertebrae. They are located in a lateral position, on the anteromedial edge of the transverse process and not on the anterior edge of the neural arch. The spinous process is long, narrow and less inclined posteriorly than in *Borhyaena* and *Prothylacynus*. Its anterior edge is straight as in *Prothylacynus* and *Borhyaena*, contrary to the condition in *Cladosictis* where it is concave anteriorly and where the spinous process is recurved anterodorsally. The major characteristic of that vertebra is the shortness of the pedicle of its neural arch, which is shorter than half of the length of the centrum, while it is longer in *Borhyaena*, *Prothylacynus*, *Cladosictis* and in didelphids. The centrum is proportionally shorter and lower than in *Borhyaena*, *Prothylacynus*, and *Cladosictis* (although to a lesser extent in this genus). The ventral side of the centrum bears a well marked crest which separates the insertions of the longi dorsi muscles as in *Cladosictis*. The condition of *Mayulestes* differs from that of *Prothylacynus* and *Borhyaena* which show no crest on the ventral side of the centrum of the anterior dorsal vertebrae. Two other anterior thoracic vertebrae are known by their centra only. They show the same characteristics as the vertebra described above.

The last two thoracic vertebrae were found associated with the first five lumbar vertebrae. Contrary to what is observed on the cervical and first thoracic vertebrae, the last thoracic is relatively much longer than in *Prothylacynus* and *Cladosictis*. On the neural arch, the prezygapophyses are oriented less dorsally than in *Prothylacynus* and the articular surface of the prezygapophyses occupies all its medial surface, while in *Prothylacynus* they are overhung by a strong metapophysis. In lateral view the postzy-

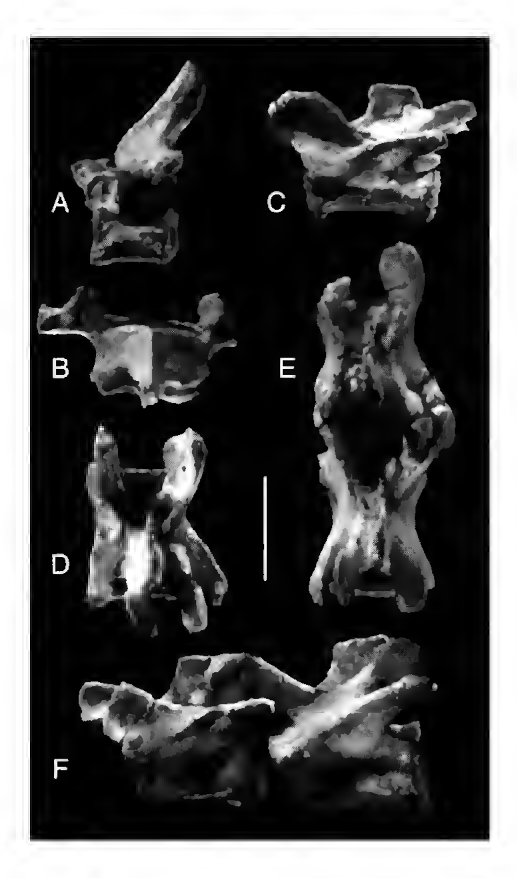


FIG. 12. — *Mayulestes ferox*, holotype (MHNC 1249). Anterior thoracic vertebra (T?1): **A**, lateral; **B**, dorsal views; T?12: **C**, lateral; **D**, dorsal views; T? 13-L1: **E**, lateral; **F**, dorsal views. Scale bar: 5 mm.

gapophyses are longer than high, contrary to those of *Prothylacynus* which are higher than long. The anterior edge of the neural spine is concave anterodorsally, its posterior edge is straight and the spine occupies the posterior two thirds of the neural arch; the neural spine is therefore slightly inclined posteriorly and the last two thoracic vertebrae of *Mayulestes* are anterior to the anticlinal vertebra. This condition differs from that of *Prothylacynus* where the neural spine of the last two thoracic vertebrae is oriented anteriorly (the vertebrae are posterior to the anticlinal vertebra) and has a straight anterior edge and a concave posterior edge. In fact, in *Prothylacynus*, the posterior part of the neural arch (*i.e.* the neural spine and the postzygapophyses) seems to have been pulled anteriorly when compared to the condition observed in *Mayulestes*. The anapophyses are proportionally longer than in *Prothylacynus* and bear, on their lateral edge, a marked ridge for the insertion of the longissimus dorsi and sacrocaudalis dorsalis muscles. This ridge is well-developed on the eleventh thoracic vertebra of *Prothylacynus* (YPM PU 15700). The centrum is relatively lower dorsoventrally than in *Prothylacynus* and its ventral surface if less rounded.

Lumbar vertebrae (Figs 12, 13)
Five lumbar vertebrae are known and, if one assumes that *Mayulestes* had six lumbar vertebrae as *Pucadelphys*, living didelphids and *Cladosictis*, it is the last lumbar which is missing since the five vertebrae were found associated. Like the thoracic vertebrae, they are relatively longer than in *Prothylacynus* and *Cladosictis*. The most remarkable feature of the lumbar vertebrae of *Mayulestes* is the shape and orientation of the neural spine. On the first three vertebrae, they are small, low, long (anteroposteriorly), oriented posteriorly and they occupy the posterior two third of the neural arch (*i.e.* their anterior edge is concave anterodorsally). The spinal process is not preserved in the fourth lumbar. The fifth lumbar has a short (anteroposteriorly) but very high neural spine which is slightly oriented anteriorly and occupies the total length of the neural arch. This vertebra is very similar to that of *Pucadelphys*. *Mayulestes* and *Pucadelphys* differ in the morphology and orientation of the neural spine from the morphology observed in the other didelphids, where the spine is generally low and oriented posteriorly or, if anteriorly, to a very slight extent. In the six lumbar vertebrae of *Cladosictis* (YPM PU 15170), the neural spines are high, short (anteroposteriorly) and strongly inclined anteriorly, and their posterior edge is concave posterodorsally. The same condition is found in the fourth, fifth and sixth lumbar of *Prothylacynus*, although in this genus the neural spine is stronger, longer (anteroposteriorly) and less inclined anteriorly than in *Cladosictis*. On the holotype of *Mayulestes*, the transverse processes are intact on the fifth lumbar only. They are more slender than those of *Prothylacynus* and *Cladosictis* (to a lesser extent in this genus) but resemble those of *Pucadelphys*. They are propor-

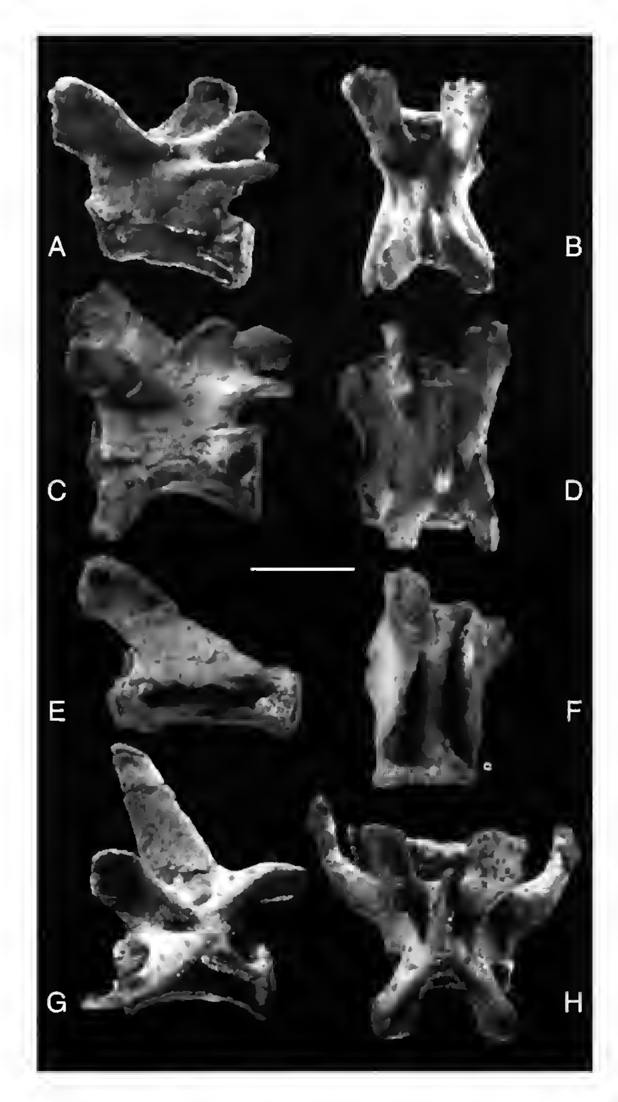


FIG. 13. — *Mayulestes ferox*, holotype (MHNC 1249). Lumbar vertebrae; L2: **A**, lateral; **B**, dorsal views; L3: **C**, lateral; **D**, dorsal views; L4: **E**, lateral; **F**, dorsal views; L5: **G**, lateral; **H**, dorsal views. Scale bar: 5 mm.

tionally longer (transversally) than those of *Prothylacynus* (which are almost complete on the fifth and sixth lumbar of YPM PU 15700) and more recurved ventrally. Their bases occupy approximately one third of the length of the centrum while they occupy half of its length in *Prothylacynus* and *Cladosictis*. The zygapophyses of the fifth lumbar vertebra are more everted than in *Prothylacynus* and form a conspicuous X-shape figure in dorsal view as observed in *Cladosictis*. As in *Prothylacynus* and *Cladosictis*, the anapophyses reduce from the first to the third lumbar vertebra; since they are small but present in the third and absent on the fifth they were either very reduced or absent on the fourth lumbar. The centra of the lumbar vertebrae are relatively slightly lower than those of *Prothylacynus* but match in this respect the condition observed in *Cladosictis*.

Sacral vertebrae

No sacral vertebrae are preserved in the holotype.

Caudal vertebrae (Fig. 14)

Four well preserved caudal vertebrae are known, two anterior and two posterior. The anterior caudal vertebrae are very similar to those of *Cladosictis*, *Borhyaena* and *Prothylacynus*. The slight differences observed could be related to their position in the tail (which cannot be defined with precision – possibly C1 and C3) rather than to the actual morphology of the taxon. When compared to *Caluromys*, the morphology of the two posterior caudal vertebrae corresponds to C7 and C8. When compared to *Pucadelphys*, the vertebrae correspond to C8 and C9 and when compared to *Cladosictis* and *Prothylacynus*, they seem to correspond to C11 and C12. They are proportionally more slender and longer than in *Cladosictis* and *Prothylacynus*. The ventral side of the centrum of both vertebrae differs from that of *Didelphis*, *Caluromys* and, to a lesser extent, *Metachirus*, which bears a ventral sulcus for the ventral median coccygeal artery. On the edges of this sulcus attaches the sacrococcygeus ventralis medialis muscle, a flexor of the tail [this sulcus does not receive the abductor muscles as stated by Marshall & Sigogneau-Russell (1995), a term which is inappropriate in the case of a flexion of the tail]. In *Mayulestes*, the sulcus is present but very weak; it is observable in the anterior and posterior third of each of the two posterior caudal vertebrae while, in the median region of the centrum, it is reduced to a flat strip. A similar condition is observed on C5 to C8 of *Pucadelphys andinus* (specimen YPFB Pal 6106) and *Monodelphis*. This feature shows some individual variation since the sulcus is more pronounced in another specimen of *Pucadelphys* (YPFB Pal 6110) whose

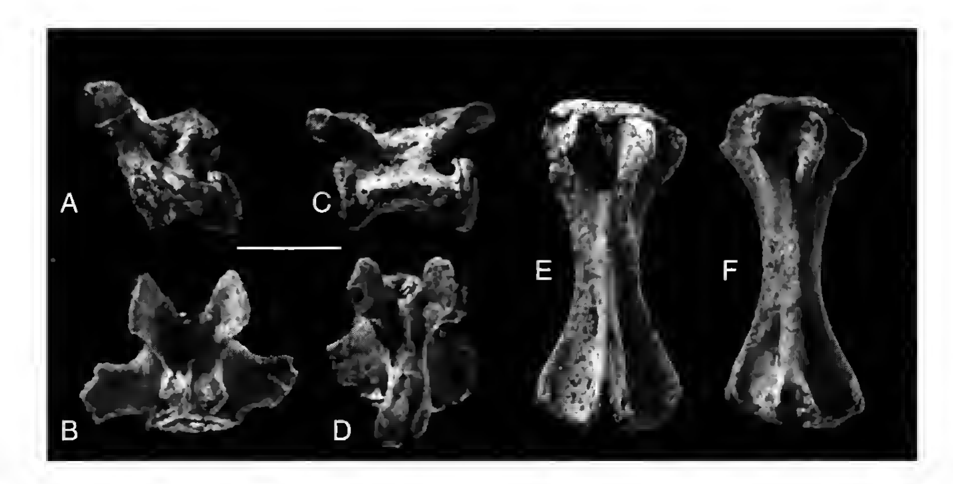


FIG. 14. — *Mayulestes ferox*, holotype (MHNC 1249). Caudal vertebrae. C?1: **A**, lateral; **B**, dorsal views; C?3: **C**, lateral; **D**, dorsal views; C?8: **E**, dorsal view; C?9: **F**, dorsal view. Scale bar: 5 mm.

C7 and C8 have been further prepared. No sulcus is observed in *Marmosa*. The anterior and posterior transverse processes of the posterior caudal of *Mayulestes* are similar in shape and relative size to those of *Caluromys* and *Pucadelphys*. They are slightly larger and more blade-like than those of *Didelphis*, *Metachirus*, *Monodelphis* and *Marmosa* where the processes are more knob-like. The morphology of the posterior caudal vertebrae of *Mayulestes* denotes an important strength of the tail musculature that could be related to prehensility (see below for discussion).

Ribs (Fig. 15)
Four ribs of the holotype of *Maylulestes* are known. Two are probably the first or second right and left ribs. They have a smaller tuberculum and a capitulum wider and flatter at its base than in *Borhyaena*. One of the other two ribs (R8?) is a relatively anterior rib since its curvature is well pronounced. It has a relatively small tuberculum and a long capitulum. It is regularly curved and does not show an angulation between the tuberculum + capitulum region and the rest of the bone, as it is observed in *Borhyaena* and *Cladosictis*. The other rib (R10 or 11) is posterior and has a weaker curvature. Both ribs were flatter than in *Borhyaena* and *Cladosictis*.

Forelimb
Scapula. (Figs 16, 17) In the following description, the spine of the scapula will be oriented vertically.
The general shape of the scapula is triangular and significantly differs from that of the other

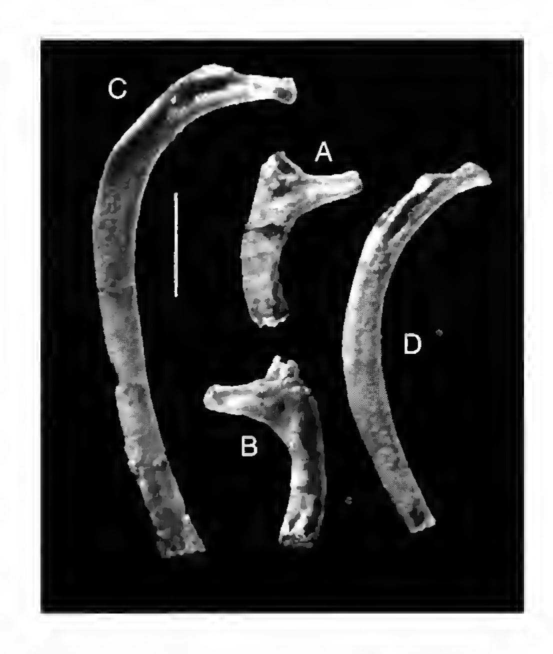


FIG. 15. — *Mayulestes ferox*, holotype (MHNC 1249). Ribs: **A**, right R1 or 2 in anterior view; **B**, left R1 or 2 in anterior view; **C**, left R?8 in posterior view; **D**, right R10 or 11 in posterior view. Scale bar: 5 mm.

borhyaenoids, *Metachirus*, *Philander* and *Didelphis* which is roughly oval-shaped or quadrangular; it shows important similarities with those of *Caluromys* and *Monodelphis*. In *Mayulestes*, the anterior edge of the scapula (*i.e.* of the supraspinatus fossa) presents a marked angulation (almost a right angle) when it is regularly convex in other borhyaenoids. The anteriorly protruding supraspinatus fossa of *Mayulestes* is very similar to those of *Monodelphis* and *Caluromys* (although a little more rounded in this genus). The posterior border of the scapula (*i.e.* of the infraspinatus fossa) is slightly concave as in *Caluromys* and is oriented posterodorsally, whereas it is convex in the other borhyaenoids and in *Didelphis*, and straight in *Pucadelphys*.

The supraspinatus fossa is much wider anteroposteriorly in its middle region than the infraspinatus fossa but is slightly shorter proximodistally. Its surface is a little superior to that of the infraspinatus fossa as observed in *Caluromys*. Both fos-



Fig. 16. — *Mayulestes ferox*, holotype (MHNC 1249). Right scapula: **A**, lateral, **B**, medial, **C**, proximal views. Scale bar: A, B, 1 cm; C, 5 mm.

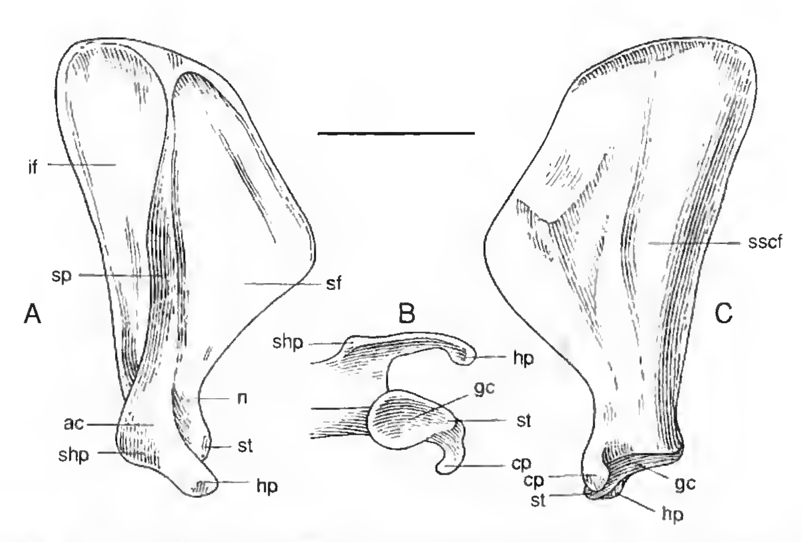


FIG. 17. — *Mayulestes ferox*, holotype (MHNC 1249). Right scapula: **A**, lateral; **B**, medial; **C**, proximal views. Abbreviations: **ac**, acromion; **cp**, coracoid process; **gc**, glenoid cavity; **hp**, hamatus process; **if**, infraspinatus fossa; **n**, neck; **sf**, supraspinatus fossa; **shp**, suprahamatus process; **sp**, spine; **sscf**, subscapular fossa; **st**, supraglenoid tubercle. Scale bar: 1 cm.

sae are very narrow in their proximal part and less extended anteroposteriorly than in the other borhyaenoids and *Didelphis*. The supraspinatus fossa is much narrower in its proximal portion than in the Santa Cruz borhyaenoids where its anteroproximal border strongly protrudes anteriorly. The morphology of the scapula of the Santa Cruz borhyaenoids is also present to a lesser extent in *Didelphis* while *Pucadelphys* resembles *Mayulestes* in this respect. The supraspinatus fossa is relatively shallow while the infraspinatus fossa is very deep, with its posterior border strongly deflected laterally, a condition common in the other borhyaenoids whose scapula is known.

The infraspinatus fossa is narrow and widens moderately toward its distal end contrary to the condition of *Prothylacynus* and *Borhyaena*. When the spine is oriented vertically, the highest point of the scapula is located almost at the posterodorsal angle of the infraspinatus fossa as in *Caluromys*, while in *Cladosictis*, *Didelphis*, *Metachirus* and *Marmosa* it is located at the dorsal extremity of the spine or at the same level as the angle. The posterodorsal angle of the scapula receives the origin of the teres major posteriorly and the insertion of the rhomboideus anteriorly.

As in *Caluromys* the spine is more elevated than in the other didelphids. It is slightly deflected posteriorly and its lateral edge is convex in anterior view. The acromion is large and forms a triangular plate which bears a long anterior process, the hamatus process, and a short posterior process, the suprahamatus process (the paracromion), located behind the anterior process. Since it is very thin and fragile, it is generally lost in fossils; it is broken in all the borhyaenoids specimens described by Sinclair (1906). In anterior view the acromion of *Mayulestes* is flat and the apex of the hamatus process is slightly bent medially. It is similar to that of *Caluromys* but it differs from that of *Didelphis* where the hamatus process is shorter and less individualised. In *Pucadelphys*, the acromion also has a long hamatus process but the whole structure is smaller than in *Mayulestes*. In medial view, the ventral extremity of the acromion is visible below the glenoid fossa as in *Pucadelphys* [although this is not shown on figure 36 of Marshall & Sigogneau-Russell (1995), it is clear in the further prepared right scapula of YPFB Pal 6106 (Fig. 18)], *Marmosa* and *Caluromys* (to a lesser extent), contrary to *Didelphis* where the acromion does not extend ventrally below the glenoid fossa. In lateral view, the hamatus process overhangs anteriorly the supraglenoid tuberosity and, in proximal view, the anterior apex of the hamatus process is slightly anterior to the cora-

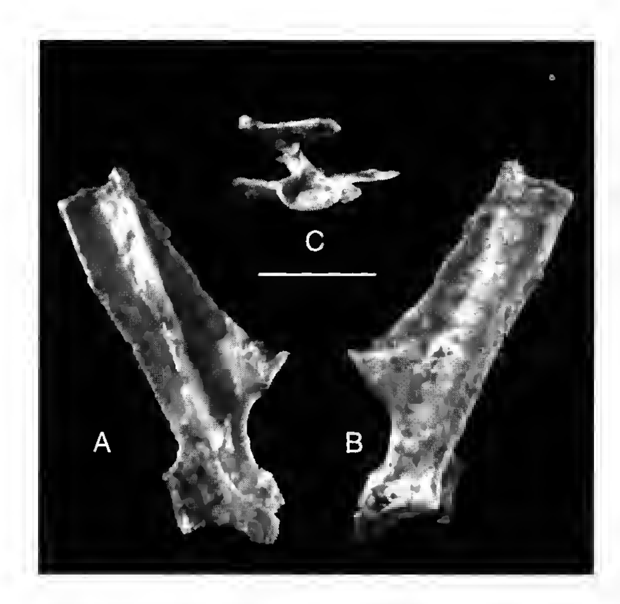


FIG. 18. — *Pucadelphys andinus* (YPFB Pal 6106). Right scapula: **A**, lateral; **B**, medial; **C**, proximal views. Scale bar: 5 mm

coid process. This condition is similar to that observed in *Caluromys* while in the other didelphids the anterior apex of the hamatus process is posterior to the anterior edge of the supraglenoid tuberosity. The condition in *Pucadelphys* is close to that observed in *Mayulestes* but the acromion is slightly less anterior than in *Mayulestes* and apparently relatively slightly larger (Fig. 18). The lateral side of the acromion bears part of the origin of the deltoideus muscle and, on the anterior border of the acromion, is inserted the atlantoacromialis muscle (= omotransversarius muscle *pro parte*).

The neck is the portion of the scapula located above the glenoid fossa at the level of the supracoracoid incisure, also called the scapular notch (which marks the ventral extremity of the supraspinatus fossa). It is long, narrow and well marked as in *Caluromys* and *Pucadelphys*, contrary to what is observed in the other borhyaenoids and *Didelphis*.

The head is small and bears an anteroposteriorly elongated glenoid cavity. It is more flattened transversally than in *Cladosictis*, *Borhyaena*, *Prothylacynus* and *Thylacinus*, but less than in *Didelphis*. The coracoid process is a small apophysis of bone strongly recurved medially, where the coracobrachialis muscle originates. The coracoid process of *Mayulestes* is longer, more slender and more recurved medially than in *Borhyaena*, *Prothylacynus*, *Cladosictis*, *Pucadelphys* and *Didelphis*. As in *Cladosictis*, it is not well separated from the supraglenoid tubercle, contrary to what is observed in *Thylacinus* and, to a lesser extent, in *Didelphis*. As in *Caluromys*, *Metachirus* and *Marmosa*, the coracoid process extends ventrally further than the supraglenoid tubercle, contrary to the condition observed in *Pucadelphys* and *Didelphis* [Marshall & Sigogneau-Russell (1995, fig. 36) have confused the coracoid process and the supraglenoid tubercle or tuber scapulae]. The supraglenoid tubercle bears the origin of the biceps brachii muscle, a powerful flexor of the elbow. On the medial side of the scapula, just dorsal to the posteromedial extremity of the glenoid cavity, is a shallow fossa for the origin of the caput longum of the triceps brachii muscle. That muscle attachment is relatively weak when compared to *Didelphis* or *Thylacinus*. However, the weakness of this attachment seems to be common in borhyaenoids since it is also little developed in *Borhyaena*, *Prothylacynus* and *Cladosictis*.

On the medial side of the scapula, the subscapularis fossa reflects the relief of the lateral side of the bone. It is strongly convex in its posterior region corresponding to the infraspinatus fossa while the relief is moderate in the anterior region. In the dog (Evans & Christensen 1979), the subscapularis fossa receives the insertion of the serratus ventralis muscle in its proximal third and the origin of the subscapularis muscle in its two distal thirds. The subscapularis is inserted on the lesser tubercle of the humerus and the serratus ventralis originates on the transverse processes of the last five cervical vertebrae. In *Didelphis*, the latter arises from the transverse processes of the last four or five cervical vertebrae (Jenkins & Weijs 1979).

Humerus. (Figs 19, 20) Both humeri of the holotype of *Mayulestes* are known. They show a significant difference in their length and proportions of their proximal epiphysis, although no pathological deformation can be observed. This variation is probably the consequence of a slight post-mortem deformation of the bones since the right humerus has been slightly compressed anteroposteriorly in its proximal half, squeezing



FIG. 19. — *Mayulestes ferox*, holotype (MHNC 1249). Right humerus: **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial; **E**, proximal views. Scale bar: A-D, 1 cm; E, 5 mm.

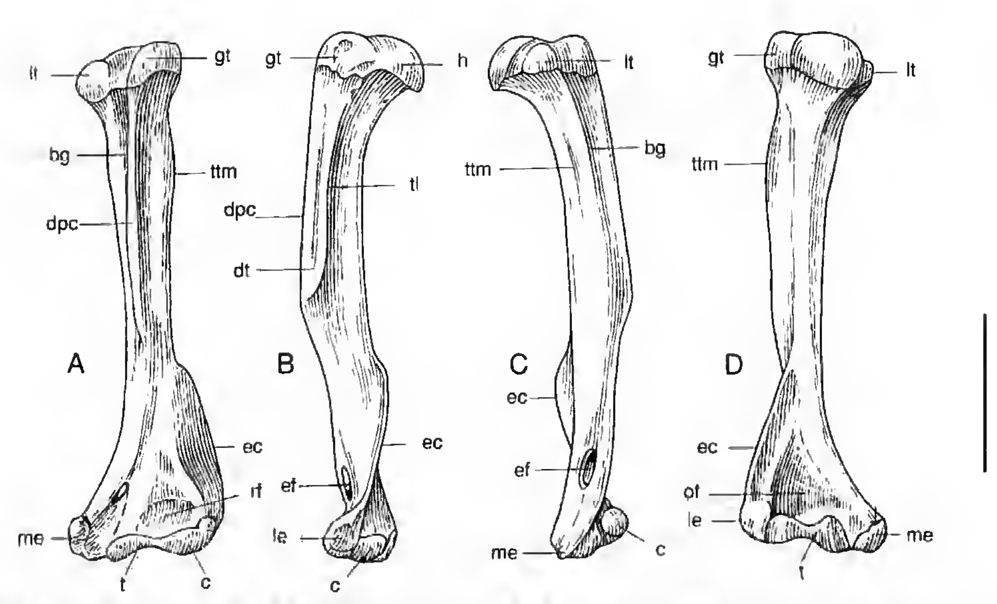


FIG. 20. — *Mayulestes ferox*, holotype (MHNC 1249). Right humerus: **A**, anterior; **B**, lateral; **C**, posterior; **D**, medial views. Abbreviations: **bg**, bicipital groove; **c**, capitulum; **dpc**, deltopectoral crest; **dt**, deltoid tuberosity; **ec**, epicondyloid crest; **ef**, entepicondylar foramen; **gt**, greater tubercle; **h**, head; **le**, lateral epicondyle; **lt**, lesser tubercle; **me**, medial epicondyle; **of**, olecranon fossa; **rf**, radial fossa; **t**, trochlea; **tl**, tricipital line; **ttm**, tuberosity for the teres major. Scale bar: 1 cm.

the epiphysis and the bicipital groove. The left humerus, which seems to have suffered very little (if any) deformation, will be referred to in the following description and comparison. The bone will be described vertically.

In proximal view, the proximal epiphysis is relatively shorter anteroposteriorly than in the genera used for comparison in this study (other borhyaenoids, didelphids and *Thylacinus*). The condyle for articulation with the scapula (the head) is slightly wider than long in *Mayulestes* as in *Pucadelphys* (Figs 21, 22), while in *Prothylacynus* it is as long as wide. In *Caluromys*, *Chironectes*, *Didelphis*, *Monodelphis* and *Marmosa* it is slightly longer than wide, and in *Metachirus* it is much longer than wide. In lateral view, the condyle has a posteroproximal orientation. However, the proximal component of this orientation is more important than in *Prothylacynus*, *Cladosictis* and *Didelphis*, whose condyle seems to be more "recurved" posteriorly. This is especially clear in the shape of the posterior side of the shaft just below the condyle, which is strongly recurved and directed distally in *Prothylacynus*, *Didelphis* and *Thylacinus*, while it is oriented posteroproximally in *Mayulestes*. This condition is also clearly observable in posterior view of the humerus where the visible portion of the condyle is much more reduced in *Mayulestes* and *Caluromys* than in the other borhyaenoids and didelphids. In fact, the orientation of the condyle of *Mayulestes* resembles more that of *Caluromys* than any other genus. The greater tubercle is slightly lower than the condyle as in *Didelphis* and *Caluromys*, while in *Prothylacynus* it is slightly higher and in *Thylacinus* it is much higher. In proximal view the greater tubercle is elongated, more than twice longer than wide and obliquely oriented. In these respects, it is similar to those of *Prothylacynus*, *Caluromys* and *Didelphis*, but differs from that of *Thylacinus* which is very thick and massive. The greater tubercle of *Mayulestes* is, however, more oblique and less salient anteriorly than those of *Prothylacynus* and *Thylacinus* where it greatly extends anteriorly, well beyond the lesser tubercle. The lesser tubercle is rounded and separated from the condyle by a sulcus. It is relatively salient anteriorly and laterally and almost reaches the level of the greater tubercle anteriorly. It is fairly similar to those of *Pucadelphys*, *Didelphis* and *Caluromys* but clearly

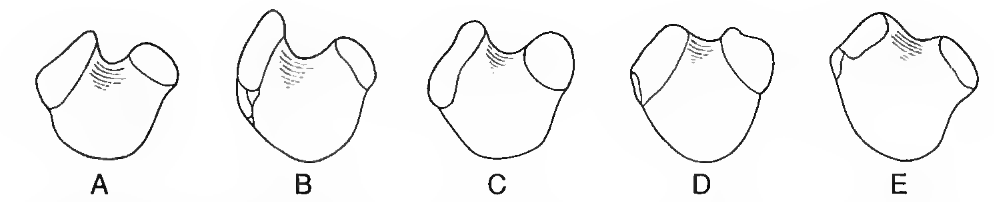


FIG. 21. — Proximal view of the proximal extremity of the humeri of: **A**, *Mayulestes*; **B**, *Prothylacynus*; **C**, *Pucadelphys*; **D**, *Caluromys*; **E**, *Didelphis*. Not to scale.

differs from that of *Prothylacynus* which is elongated, obliquely oriented, appressed against the condyle, and which remains far behind the greater trochanter anteriorly. These conditions of *Prothylacyinus* are observed in the dog, a terrestrial cursorial carnivoran.

The bicipital groove is well marked and faces anteromedially. It extends on the anterior side of the shaft of the bone where it is deeper than in *Prothylacynus*, *Caluromys* and *Didelphis*. Laterally, below the greater tubercle, on the proximal 40% of the length of the shaft, there is a sharp and elevated tricipital line. It is more developed and more salient laterally than in *Prothylacynus* and *Didelphis*, where it is very weak, but resembles that of *Pucadelphys* which is very prominent.

On the anterior side of the proximal two thirds of the shaft, the deltopectoral crest runs distally from the anteromedial angle of the greater tubercle on approximately 60% of the length of the bone. The deltopectoral crest is relatively narrow, salient and slightly concave laterally. It resembles those of *Didelphis* and *Caluromys* but differs from that of *Pucadelphys* which is shorter, and from that of *Prothylacynus* which is much thicker and straight; the latter features are even more pronounced in *Thylacinus*. The deltopectoral surface, limited by the deltopectoral crest anteriorly and the tricipital line posteriorly, is relatively wide and concave and faces more anteriorly than laterally. In these respects it resembles that of *Pucadelphys* and living didelphids but differs from those of *Prothylacynus* and *Thylacinus* which are narrow, flat or convex and face more laterally than anteriorly. On the anterior border of the tricipital line, on its proximal half, is a very salient crest oriented laterally and which receives the origin of the caput lateralis of the triceps brachii. This tricipital crest approaches the condition observed in *Pucadelphys* and *Monodelphis*, although it is slightly less salient in these genera. It differs from those of *Prothylacynus*, *Didelphis* and *Thylacinus* which are much weaker.

On the medial side of the proximal third of the diaphysis, below the lesser tubercle, is a relatively weak tuberosity for the teres major muscle as in *Didelphis*, and the fossa posterodistal to the lesser tubercle is small and shallow. That region of the humerus of *Mayulestes* strongly differs from that of *Prothylacynus* where the tuberosity for the teres major is very large and salient, and forms a sharp crest which runs proximally towards the lesser tubercle and forms a deep fossa located distally to the posterolateral angle of the lesser tubercle and the posteromedial side of the condyle. Laterally, the fossa is limited by a wide and rounded ridge which runs distally from the posterior edge of the condyle along the proximal half of the posterior side of the diaphysis. On the proximal extremity of the fossa and the ridge is located the origin of the accessory head of the triceps which was very strong in *Prothylacynus*. Since in *Mayulestes* the relief of the attachments of this muscle was intermediate between those of *Didelphis* and *Caluromys* on the one hand and *Prothylacynus* on the other hand, it is likely that the muscle was stronger than in the former but much weaker than in the latter.

The distal extremity of the humerus is markedly flattened anteroposteriorly and plate-like as in all the borhyaenoids and didelphids. The epicondyloid crest is very large and extends along about 30% of the diaphysis; its proximal extremity reaches a point, on the shaft, lateral to the distal extremity of the deltopectoral crest as in

Prothylacynus. This point of the shaft is located more proximally than in *Prothylacynus*. In *Cladosictis*, the distal extremity of the deltopectoral crest is in a far more distal position than in *Prothylacynus* and *Mayulestes* and reaches the distal quarter of the bone; in this genus, the proximal extremity of the epicondyloid crest is located more proximally than the distal extremity of the deltopectoral crest. In *Mayulestes* the proximal extremity of the epicondyloid crest has a regular concavoconvex contact with the diaphysis as in *Cladosictis*, *Metachirus* and *Marmosa* and is not recurved anteriorly; it differs from the condition of *Prothylacynus*, *Pucadelphys*, *Didelphis* and *Caluromys* whose epicondyloid crest is limited proximally by a marked notch and recurved anteriorly in that region.

On the medial side of the humerus, the entepicondyle is very long and strongly projected distomedially, more than in *Prothylacynus*, *Cladosictis* and much more than in *Didelphis* and *Caluromys*. It resembles the condition observed in *Pucadelphys*. It almost reaches the level of the medial crest of the trochlea distally (Fig. 22) as in *Pucadelphys*, contrary to the condition observed in *Prothylacynus* and most living didelphids. Its apex, where the flexors of the carpus and digits originate, is rounded and subcircular as in *Prothylacynus* and *Pucadelphys* and not elongated and oval-shaped (in proximodistal view) as in *Didelphis* and *Caluromys*. The ridge of bone that unites the distal extremity of the deltopectoral crest with the apex of the entepicondyle and passes above the entepicondylar foramen is more salient anteriorly than in *Didelphis*, *Caluromys*, *Prothylacynus* and *Cladosictis*, which contributes to give a more twisted aspect to that part of the humerus of *Mayulestes* than in the genera cited above. *Mayulestes* resembles *Pucadelphys* in this respect. On the anterior side of the bone, just proximal to the capitulum, is a radial fossa deeper than in *Prothylacynus*, *Cladosictis*, *Didelphis* and *Caluromys*.

The entepicondylar foramen is large and oval-shaped. It is proportionally similar in size and shape to those of *Prothylacynus*, *Cladosictis*, *Didelphis* and *Caluromys*. The groove for the passage of the median artery (the internal articular sulcus of Osgood 1921), located between the medial border of the trochlea and the lateral edge of the epicondyle, is deeper than in *Didelphis*, *Caluromys* and *Cladosictis* but resembles that of *Prothylacynus*. On the posterior side of the bone, the olecranon fossa is much shallower than in *Prothylacynus*, *Cladosictis* and *Didelphis* but a little deeper than in *Caluromys* where it is very shallow. In posterior view, the trochlea has relatively well marked crests as observed in *Didelphis*, but not as sharp and salient as in *Prothylacynus*. As in *Didelphis*, the

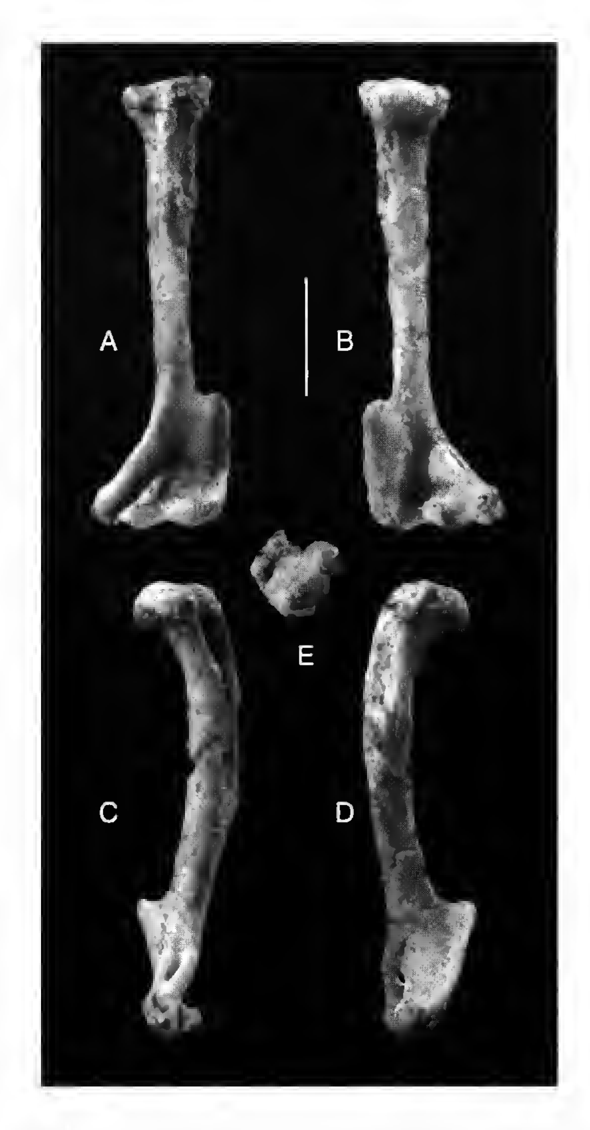


Fig. 22. — *Pucadelphys andinus* (YPFB Pal 6106). Left humerus: **A**, anterior; **B**, posterior; **C**, medial; **D**, lateral, **E**, proximal views. Scale bar: 5 mm.

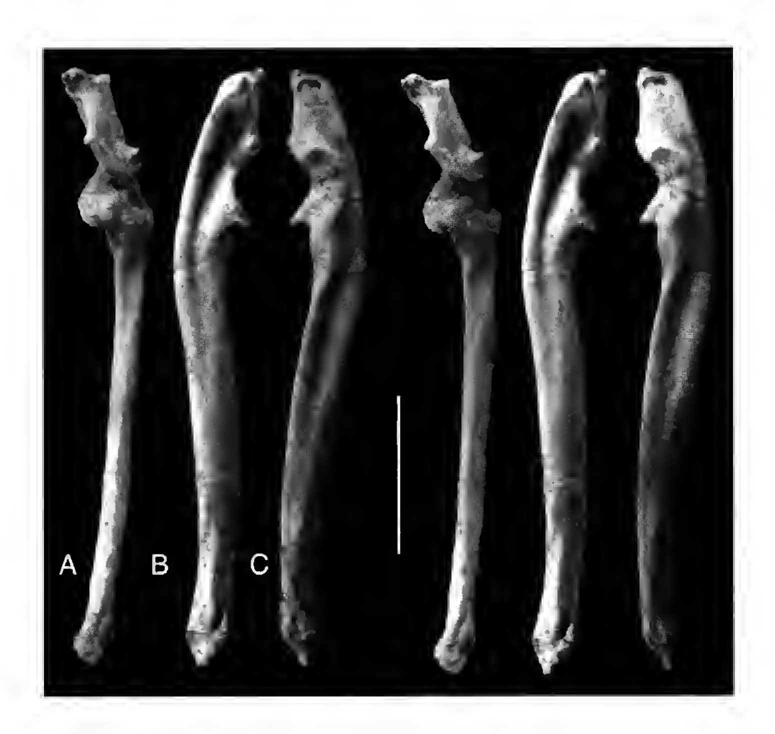


FIG. 23. — *Mayulestes ferox*, holotype (MHNC 1249). Left ulna: **A**, anterior; **B**, lateral; **C**, medial views. Scale bar: 1 cm.

trochlea of *Mayulestes* is deeper than in *Prothylacynus*; it greatly differs from the trochlea of *Caluromys* which is wider, deeper and has lower crests than in *Mayulestes*. The capitulum is more salient and convex than in *Prothylacynus* and *Cladosictis*, less than in *Caluromys* and *Pucadelphys*, but resembles that of *Didelphis*. In *Prothylacynus* the capitulum is less elongated transversely, longer proximodistally and, as a whole, more rounded. The distal articular surface of *Pucadelphys* differs from that of *Mayulestes* in its slightly narrower trochlea with a lower medial crest and its wider capitulum.

Ulna. (Figs 23, 24) The bone is notably short, as are those of *Borhyaena*, *Prothylacynus* and *Cladosictis*, and differs from the longer ulnae of *Thylacinus*, *Didelphis* and *Caluromys*. The proximal half of the bone is markedly recurved anteriorly as in *Pucadelphys* (Fig. 25). It strongly differs from those of *Prothylacynus* and *Cladosictis*, which have a globally straight ulna with a posterior border concave in its middle third, and from those of *Borhyaena* and *Thylacinus*, which are bent posteriorly. It resembles the condition observed in *Caluromys* but differs from that of *Didelphis* where the proximal extremity is only slightly bent anteriorly.

In anterior view, the olecranon and the articular area are markedly deflected medially as it is observed, to a lesser extent, in *Borhyaena*, *Pucadelphys* and *Didelphis* but contrary to *Prothylacynus*, *Cladosictis*, *Thylacinus* and *Caluromys*. In lateral view, the posterior and proximal edges of the olecranon of *Mayulestes* form an angle of more than 120°. It resembles that of *Caluromys* where the angle is smaller but clearly greater than 90°. It differs from those of *Borhyaena*, *Prothylacynus*, *Cladosictis*, *Thylacinus*, *Didelphis*, *Chironectes*, *Metachirus* and *Caluromys* which almost form a right angle, sometimes a little less than 90° as in *Borhyaena*, or a little more, as in *Didelphis*. The condition of *Marmosa* and *Pucadelphys* is close to that of *Mayulestes*. In anterior view, the olecranon is long as observed in *Borhyaena*, *Prothylacynus*, *Cladosictis* and *Thylacinus*. It is slightly longer than in *Didelphis*, *Caluromys* and *Chironectes*. The medial side of the olecranon and proximal half of the shaft bear

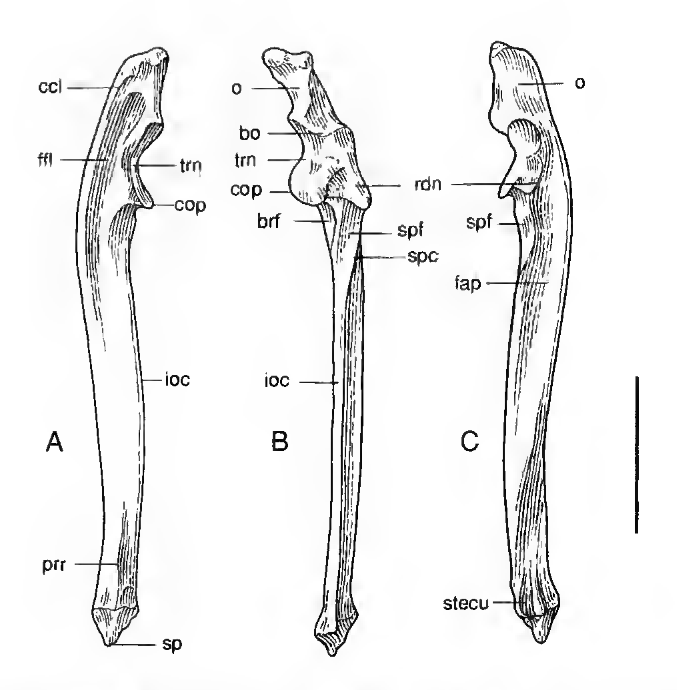


FIG. 24. — *Mayulestes ferox*, holotype (MHNC 1249). Left ulna: **A**, medial; **B**, anterior; **C**, lateral views. Abbreviations: **bo**, beak of the olecranon; **brf**, brachialis fossa; **cop**, coronoid process; **ccl**, crest for attachment of the posterior and transverse part of the ulnar collateral ligament; **fap**, fossa for the abductor pollicis longus and extensor indicius propius; **ffl**, fossa for the flexor digitorum profundus; **ioc**, interosseous crest; **o**, olecranon; **prr**, pronator ridge; **rdn**, radial notch; **sp**, styloid process; **spc**, supinator crest; **spf**, supinator fossa; **stecu**, sulcus for the tendon of the extensor carpii ulnaris; **trn**, trochlear notch. Scale bar: 1 cm.

a very deep fossa for the flexor carpii ulnaris and flexor digitorum profundus. That fossa is much deeper than in any of the three borhyaenoid compared here to *Mayulestes* (although *Prothylacynus* has a deeper fossa than *Cladosictis* and *Borhyaena*). The fossa of *Mayulestes* is also deeper than in *Didelphis* but approaches the condition observed in *Caluromys* and *Marmosa*. The flexor fossa is limited posteriorly and proximally by an extremely strong crest for the attachment of the posterior and transverse parts of the ulnar collateral ligament.

In medial view, the trochlear notch (= greater sigmoid cavity = articular surface for the humerus) is relatively wide open (in medial view) and shallow as in *Caluromys* (although to a greater extent than in this latter genus). It differs from *Borhyaena*, *Prothylacynus*, *Thylacinus*, *Cladosictis*, *Didelphis*, *Chironectes* and *Metachirus*, where the trochlear notch is very deep, concave and less open (although this is less marked in *Cladosictis*), but strongly resembles the condition observed in *Caluromys*. In anterior view, the beak of the olecranon (the proximal crest of the trochlear notch) is less salient than in the other borhyaenoids but more than in *Caluromys*; it approaches the condition of *Didelphis*. Its width is greater in *Mayulestes* than in didelphids but resembles in this respect the condition observed in other borhyaenoids. The coronoid process, the medial extension of the distomedial portion of the trochlear notch, is large and oriented mediodistally. It differs from that of the Santa Cruz borhyaenoids which is stronger, longer and protrudes medially. Among didelphids, it resembles that of *Caluromys* in this respect and differs from those of *Pucadelphys*, *Didelphis* and *Metachirus*. The radial notch (= lesser sigmoid cavity = articular surface for the radius) is located distal and lateral to the trochlear notch (articular surface for the humerus) and faces anterolaterally. The line of contact between the humeral and radial surfaces has an anteromedial-posterolateral orientation. It is a low ridge anteromedially and it is flat and

continuous posterolaterally. In other words, the radial and humeral facets have an angular contact anteromedially and a flat contact posterolaterally. In the other borhyaenoids and in *Thylacinus*, the radial notch is always separated from the trochlear notch by a sharp crest anteromedially and by a small ridge posterolaterally (*i.e.* the angle between the two articular surfaces is more pronounced). In *Prothylacynus*, *Borhyaena* and *Thylacinus* the angle between the anteromedial contact of both articular surfaces (in anterior view) is equal to or smaller than 90°; it is more than 120° in *Mayulestes*. In the Didelphidae the angle varies around 90° but can be close to 120° in some specimens of *Didelphis* or more in *Caluromys*. The radial notch is shallow and does not excavate the anterolateral face of the ulna as in the Santa Cruz borhyaenoids and *Thylacinus*. It is roughly triangular and not divided into two portions by a proximal inflexion of its distal border as observed in the other borhyaenoids and *Thylacinus*. In *Mayulestes* and *Caluromys*, this articular surface is almost parallel to the diaphysis, but, contrary to what is observed in *Mayulestes*, the medial part of the radial notch in *Caluromys* is not in contact with the trochlear notch anteromedially.

Distal to the coronoid process on the anteromedial side of the ulna is a well-developed laterally oriented fossa, for the insertion of the brachialis and biceps muscles. It differs from that of didelphids which is slightly larger and faces anteriorly. On the anterior face of the diaphysis, laterally, is a well marked supinator crest which runs distally from the lateral edge of the radial articulation. Between this crest and the lateral border of the brachialis fossa is an elongated depressed area facing anterolaterally. This fossa and the supinator crest probably represent the origin of the supinator (= supinator brevis). This muscle is absent in *Didelphis* (Coues 1872) and probably also in the other living didelphids since none of them has a true supinator crest and fossa. In didelphids, the supination function is performed by the brachioradialis. In *Cladosictis*, the supinator crest is present but smaller than in *Mayulestes* and this structure is even smaller in *Prothylacynus* and *Thylacinus*. It is absent in *Borhyaena*.

On the anterolateral edge of the shaft is a robust



Fig. 25. — *Pucadelphys andinus*, holotype (YPFB Pal 6105). Left ulna: **A**, anterior; **B**, lateral; **C**, medial views. Scale bar: 5 mm.

interosseous crest which is in continuity with the supinator crest. It is more salient than in *Didelphis*, *Metachirus* and *Borhyaena* where it is fairly rounded. It is clearly not as sharp as in *Caluromys* but approaches the condition of *Prothylacynus*. On the lateral side of the shaft is an elongated depression, relatively deep in the middle third of the shaft but becoming shallower in its distal extremity. This area corresponds to the origin of the abductor pollicis longus and probably to the extensor indicus proprius [the extensor pollicis longus is absent in *Didelphis* (Coues 1872) and probably in didelphids in general]. The lateral fossa of the ulna of *Mayulestes* is deeper than in most of the living didelphids, except *Caluromys* where the fossa is more pronounced. The condition of *Mayulestes* is similar to those of *Prothylacynus* and *Cladosictis* but clearly differs from those of *Borhyaena* and *Thylacinus* where the fossa is very reduced.

On the medial side of the distal quarter of the diaphysis is a well-developed crest for the origin of the pronator quadratus. It is sharper than in the Santa Cruz borhyaenoids and approaches the condition observed in *Pucadelphys* and some living didelphids (*Didelphis*, *Monodelphis*). On



Fig. 26. — *Mayulestes ferox*, holotype (MHNC 1249). Left radius: **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial; **E**, proximal; **F**, distal views. Scale bar: A-D, 1 cm; E-F, 5 mm.

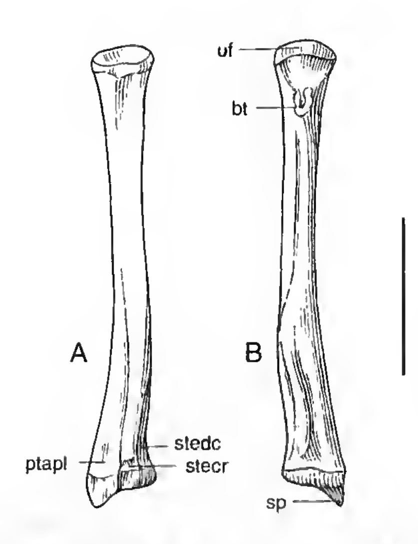


Fig. 27. — *Mayulestes ferox*, holotype (MHNC 1249). Left radius: **A**, anterior; **B**, posterior views. Abbreviations: **bt**, bicipital tuberosity; **ptapl**, passage of the tendon for the abductor pollicis longus; **sp**, styloid process; **stecr**, sulcus for the tendon of the extensor carpii radialis; **stedc**, sulcus for the tendon of the extensor digitorum communis; **uf**, ulnar facet. Scale bar: 1 cm.

the anterolateral side of the distal extremity of the diaphysis is a shallow groove which extends on the epiphysis and probably received the tendon of the extensor carpii ulnaris. This structure is absent in *Cladosictis*, *Borhyaena* and *Thylacinus*. It is well-developed in *Prothylacynus*, *Didelphis* and *Caluromys*.

The styloid process of the ulna of *Mayulestes* is small, regularly conical and flattened anteroposteriorly. It differs from those of the other borhyaenoids which are more rounded and bear a clear anteromedial notch.

Radius. (Figs 26, 27) The bone is short as the ulna and markedly recurved posteriorly like those of *Prothylacynus*, *Cladosictis*, *Thylacinus*, *Didelphis* and *Caluromys*, but differs from that of *Borhyaena* which is relatively straight. As preserved, the humeral facet is strongly oval-shaped (almost twice longer than wide) and resembles those of *Cladosictis*, *Borhyaena* and *Thylacinus* but differs from the humeral facets of *Prothylacynus*, *Didelphis* and *Caluromys* which tend to be less elongated transversally. However, it is likely that the anterior border of the articular facet has been slightly eroded (and perhaps anteroposteriorly compressed) during fossilisation. Therefore, it is probable that the humeral articular facet of the radius of *Mayulestes* was slightly less transverse than what is actually observed on the only known radius of *Mayulestes*, possibly approaching the condition

of the living didelphids. The ulnar facet is very short proximodistally. It is shorter than in *Prothylacynus*, *Cladosictis* and *Borhyaena* and much shorter than those of *Didelphis* and *Caluromys*. The bicipital tuberosity is weak; it is smaller and located further distally on the shaft than in *Borhyaena* and *Cladosictis* but resembles the condition of *Prothylacynus*. On the lateral edge of the distal half of the shaft is a conspicuous ridge limited by shallow grooves anteriorly and posteriorly and where the radial part of the origin of the abductor pollicis longus probably inserted. This ridge is better marked than in *Borhyaena*, *Cladosictis*, *Thylacinus* and *Didelphis* but considerably weaker than in *Prothylacynus* and *Caluromys*. In the latter, it extends as a very thin and salient blade from the distal border of the bicipital tuberosity (a little more distal in *Prothylacynus*) to the lateral side of the distal extremity of the shaft.

The distal epiphysis bears a well-developed styloid apophysis which is better individualised than in *Borhyaena* and *Cladosictis* and larger than in *Didelphis* and *Caluromys*. It roughly resembles that of *Prothylacynus*. On the anterior side of the distal epiphysis, lateral to the styloid process, are two shallow grooves for the passage of the tendon of the extensor carpi radialis medially and extensor digitorum communis laterally. The medial side of the styloid process is a flat area that transmitted the tendon for the abductor pollicis longus. Those structures are better individualised than in the other borhyaenoids but a little less than in *Didelphis*; their development is similar to that observed in *Caluromys*. In distal view of the bone, the distal epiphysis is flattened anteroposteriorly, the scapholunar articulation is oval-shaped, very concave, and the styloid process is located anteromedially. It differs from the condition of the other borhyaenoids, *Thylacinus* and *Didelphis*, where the scapholunar articulation is shallower and where the styloid process is generally thicker and located medially. It resembles the condition observed in *Caluromys* although in this genus the styloid process is located medially and the articular surface is shallower and wider. The distal epiphysis of the radius of *Mayulestes* is not thickened medially and, on its lateral side, the ulnar facet is hardly discernible.

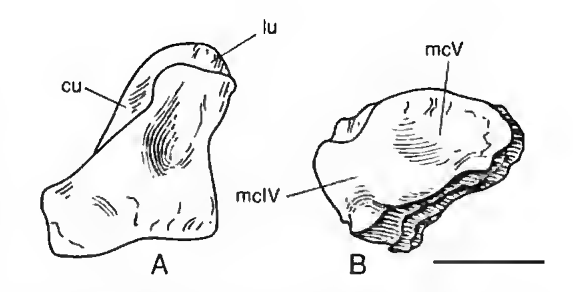


Fig. 28. — *Mayulestes ferox*, holotype (MHNC 1249) Unciform: **A**, dorsal; **B**, proximal views. Abbreviations: **cu**, articular facet with the cuneiform; **lu**, articular facet with the lunar; mcIV, articular facet with the mcIV; mcV, articular facet with the mcV. Scale bar: 2 mm.

The lateral side of the distal extremity of the shaft is not thickened and not excavated to receive ulna.

Carpus. (Fig. 28) The only bone known of the carpus of *Mayulestes* is the right unciform. The anterior side of the bone is roughly triangular with a developed medioproximal process which articulates with the lunar as in *Didelphis*. The unciform of *Borhyaena* (YPM PU 15701) (Sinclair 1906, pl. 54, fig. 4) is partially broken. However, it appears to have been more quadrate in anterior view and the lunar process must have been more massive than in *Mayulestes*. The articular facet for the cuneiform is very sigmoid and faces proximolaterally as in *Didelphis* while it faces more proximally in *Borhyaena*. The articular facet for the McIV and V is triangular as in *Didelphis* and *Borhyaena*.

Metacarpus. (Fig. 29) The left McIII of the holotype is preserved. It is incomplete and lacks the distal epiphysis. On the proximal epiphysis, the articular facet for the McIV is more concave than in *Cladosictis* and *Didelphis*. Contrary to the condition observed in *Didelphis*, the part of the epiphysis which bears this facet protrudes laterally.

The left McV of the holotype is known. It is more slender and longer than those of *Cladosictis* (YPM PU 15046), *Sipalocyon* (YPM PU 15154) and *Borhyaena* (YPM PU 15701). The bone is flattened dorsoplantarly, a feature which is not found in the Santa Cruz borhyaenoids and didelphids. The epiphyses are flattened in the same plane, *i.e.* their main axes are parallel. As a result, when the proximal epiphysis articulates

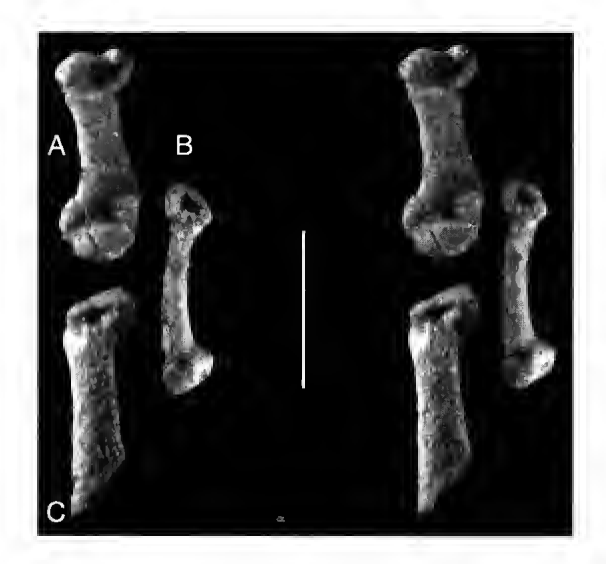


Fig. 29. — *Mayulestes ferox*, holotype (MHNC 1249). McV: **A**, dorsal; **B**, medial views; McIII: **C**, dorsal view. Scale bar: 5 mm.

with the McIV, the flexion axis of the distal epiphysis of the McV tends to be closer to a perpendicular than to a parallel position in relation to the dorsopalmar plane of the manus. Therefore, the plane of articulation of digit V tends to be perpendicular to that of digit III. In *Didelphis*, the proximal epiphysis is flattened transversely and roughly perpendicular to the dorsopalmar plane. However, the plane of the distal epiphysis is not parallel that of the proximal (as in *Mayulestes*) and the articulation plane of digit V makes an angle of approximately 120° with that of digit III. The medial surface of the proximal epiphysis (which articulates with the McIV) is very salient in *Mayulestes*, and almost forms a small condyle thus indicating a good mobility of the finger (especially abduction and adduction). This articulation is less convex in *Didelphis*. On the distal epiphysis, in *Mayulestes*, the condyle is smaller but more convex than in *Didelphis* and there is a well marked articular fossa, while it is almost absent in *Didelphis*. This condition denotes a greater mobility of the fingers in *Mayulestes*. Furthermore, as in *Didelphis* but to a greater extent, the distal epiphysis is recurved medially. In *Sipalocyon* and *Cladosictis* the McV are straight and in *Borhyaena* the distal epiphysis is recurved laterally.

Hindlimb

Pelvis. (Figs 30, 31) The major characteristic of the pelvis consists in the shape and proportions of its ilium. The ilium is approximately 57% of the total length of the bone as in *Cladosictis* (in YPM PU 15170). It is similar to the condition found in *Thylacinus* (AMNH 35244) where the ilium is approximately 54% of the total length of the bone but significantly differs from *Didelphis* and *Caluromys* where the proportions are 66% and 67% respectively. The body of the ilium (the portion of the bone between the wing anteriorly and the acetabulum posteriorly) is longer and more slender than in *Cladosictis*, *Prothylacynus* and *Thylacinus* but it is shorter than in *Caluromys*. It is fairly similar to that of *Didelphis* and *Pucadelphys*. The wing is longer than in *Pucadelphys* but shorter than in *Didelphis*, *Marmosa* and *Caluromys*. It approximates the relative size and proportions observed in *Prothylacynus* and *Cladosictis*.

In lateral view, the wing of the ilium has a roughly rectangular outline. Its dorsal edge is slightly convex and its ventral edge is weakly concave. In this respect it approaches the condition observed in *Cladosictis* and *Thylacinus*. However, in these genera, as well as in *Prothylacynus*, the profile of the dorsal edge of the ilium is less salient dorsally, and gives the wing a more triangular morphology.

The posterodorsal iliac spine is well marked in *Mayulestes* but it is much less developed than in *Cladosictis* and in *Prothylacynus*, where it is extremely salient and forms the anterior edge of a very deep greater sciatic notch. The anterodorsal iliac spine is virtually absent in *Mayulestes* and that angle of the ilium is rounded and certainly does not deserve the name of spine. In *Prothylacynus*, *Cladosictis* and *Thylacinus*, the anterodorsal angle of the ilium is even more rounded than in *Mayulestes* and gives the ilium a ventrally deflected shape. This is emphasised by the morphology of the ventral edge of the ilium, more concave in *Prothylacynus*, *Cladosictis* and *Thylacinus* than in *Mayulestes*. Furthermore, the anteroventral iliac spine is much more salient in *Prothylacynus*, *Cladosictis* and *Thylacinus* than in *Mayulestes*. On the medial side of the iliac spine are inserted the quadratus lumborum (also on



FIG. 30. — *Mayulestes ferox*, holotype (MHNC 1249). Right innominate: **A**, lateral; **B**, dorsal; **C**, ventral views. Scale bar: 1 cm.

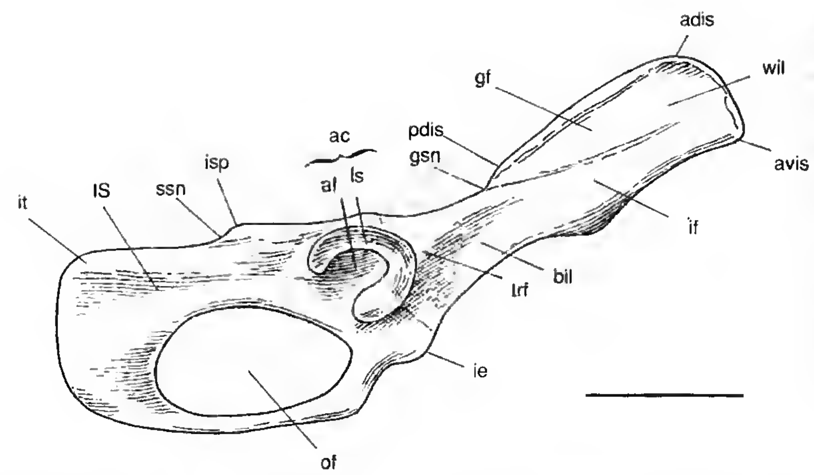


FIG. 31. — *Mayulestes ferox*, holotype (MHNC 1249) Right innominate in lateral view. Abbreviations. **ac**, acetabulum; **adis**, anterodorsal iliac spine; **af**, acetabular fossa; **avis**, anteroventral iliac spine; **bil**, body of the ilium; **gf**, gluteal fossa; **gsn**, greater sciatic notch; **ie**, iliopubic eminence; **if**, iliac fossa; **IL**, ilium; **IS**, ischium; **isp**, ischiatic spine; **it**, ischiatic tuberosity, **ls**, lunate surface; **of**, obturator foramen; **pdis**, posterodorsal iliac spine; **ssn**, smaller sciatic notch; **trf**, tuberosity for the rectus femoris; **wil**, wing of the ilium. Scale bar: 1 cm.

the ventromedial border of the ilium), a powerful flexor of the vertebral column and part of the erector spinae (also on the dorsomedial face of the ilium), the major extensor of the vertebral column. In *Mayulestes*, a small iliac tuberosity or posteroventral iliac spine is present while it is absent in *Prothylacynus*, *Cladosictis* and *Thylacinus*. In *Didelphis* and *Caluromys*, the ilium is longer and narrower than in *Mayulestes* and the iliac spines are relatively smooth, like in *Mayulestes*. In *Pucadelphys*, the ilium has an intermediate morphology between those of *Mayulestes* and the Santa Cruz borhyaenoids: as in the former, there is a clear posteroventral iliac spine but, as in the latter, the posterodorsal iliac spine is more salient than in *Mayulestes*, the greater sciatic notch is well marked, and the very rounded anterodorsal angle and the concave ventral edge of the ilium give the bone a ventrally deflected morphology.

The lateral side of the wing of the ilium of *Mayulestes* bears a low and rounded ridge which arises from the body of the ilium, runs anteriorly and vanishes in the anterior third of the wing. That ridge is absent in *Prothylacynus* and *Cladosictis* and very poorly marked in *Thylacinus*. In *Caluromys*, the ridge is more pronounced than in *Mayulestes* and reaches the anterior extremity of the ilium; it is extremely salient in *Didelphis* and divides the lateral side of the bone into two well defined fossae. The superior fossa mainly receives the origin of the gluteus medius (gluteal fossa) and the lower that of the iliacus (iliac fossa). In *Mayulestes*, the two fossae are approximately of the same size as in living didelphids, while in *Pucadelphys* the gluteal fossa is clearly larger than the iliac fossa. In dorsal view, the wing of the ilium is thin as in *Pucadelphys* and conspicuously everted as in *Cladosictis*, *Prothy-lacynus* and *Pucadelphys*, contrary to *Didelphis*, *Marmosa* and *Caluromys* where the bone is almost straight. On the medial side of the ilium the articulation with the sacrum is very little marked but it seems that only one sacral vertebra was articulating with the bone as in *Cladosictis* and *Thylacinus* rather than two as in *Didelphis* and *Caluromys*. As in *Pucadelphys* and *Cladosictis*, the wing of the ilium is more everted than in the living didelphids. The important eversion of the ilium provides a larger insertion area for the erector spinae.

On the lateral side of the body of the ilium, just anterior to the acetabulum, the tuberosity for the rectus femoris is small. It is, however, slightly larger than those of *Caluromys* and *Didelphis* but differs from those of *Prothylacynus* and *Cladosictis* which are large and very salient. In *Thylacinus*, the tuberosity is not as developed as in these genera but it is larger than in *Mayulestes*. It is also relatively large in *Pucadelphys*. On the ventral side of the pelvis of *Mayulestes*, at a point which corresponds to the junction of the ilium and the pubis, is a small tuberosity, the iliopubic eminence where is attached the tendon of the psoas minor, a flexor of the lumbar part of the vertebral column. The iliopubic eminence of *Mayulestes* is weaker than in *Cladosictis* and *Prothylacynus* but more developed than in *Didelphis* and *Caluromys* where it is sometimes totally absent.



FIG. 32. — *Mayulestes ferox*, holotype (MHNC 1249). Left femur: **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial; **E**, proximal. Right femur: **F**, anterior; **G**, posterior; **H**, distal views. Scale bar: A-D, F, G, 1 cm; E, H, 5 mm.

The acetabulum is shallower and more open than in *Cladosictis*, *Prothylacynus* and *Didelphis*. It similar to that of *Caluromys* and indicates a greater mobility at the articulation. The lunate surface is the articular surface with the femur; it is composed of a ventral and a dorsal lobe separated by the acetabular fossa. In *Mayulestes* the dorsal lobe of the lunate surface is smaller and narrower than the ventral one. The same condition exists in *Caluromys*, *Didelphis* and *Pucadelphys* while in *Cladosictis* and *Prothylacynus* both lobes are approximately the same size and in *Thylacinus* the dorsal lobe is longer and wider than the ventral one. The anterior border of the acetabulum is salient laterally and thickened; the dorsal border, in dorsal view, is well excavated (*i.e.* concave laterally). The condition of *Mayulestes* is similar to that of *Caluromys*, *Phalanger*, *Petaurus* and *Pucadelphys*, but differs from those of *Cladosictis*, *Prothylacynus*, *Metachirus* and *Didelphis*.

The ishium is longer than in the Didelphidae and similar in size to that of *Cladosictis*. On the dorsal edge of the bone, posterior to the acetabulum, is a small tubercle, the ischiatic spine. In *Mayulestes* it is slightly larger than in *Caluromys*, *Didelphis* and *Pucadelphys*, but slightly less developed than in *Cladosictis*, *Prothylacynus* and *Thylacinus*. Posterior to the ischiatic spine is the smaller sciatic notch which, consequently, is less pronounced in *Mayulestes* than in the Santa Cruz borhyaenoids. In its posterior portion, the



ischium of *Mayulestes* is longer and narrower than in *Caluromys* and *Didelphis* but resembles in these respects the condition observed in *Cladosictis*. The posterodorsal angle of the ischium is the ischiatic tuberosity where originate the biceps femoris and the semitendinosus, both extensors of the thigh. The ischiatic tuberosity is weak in *Mayulestes* and *Caluromys*. It is stronger in *Didelphis* and *Cladosictis* and much stronger in *Thylacinus*.

The posterodorsal angle of the ischium is not modified in a true ischiatic tuberosity and is not slightly recurved ventrolaterally as it is observed in didelphids. In *Cladosictis* and *Prothylacynus* they are more developed than in *Mayulestes* and, in *Thylacinus*, it is stronger than in the former genera. The ischiatic tuberosity of didelphids is reduced but a little stronger in *Didelphis*, *Metachirus* and *Monodelphis* than in the other

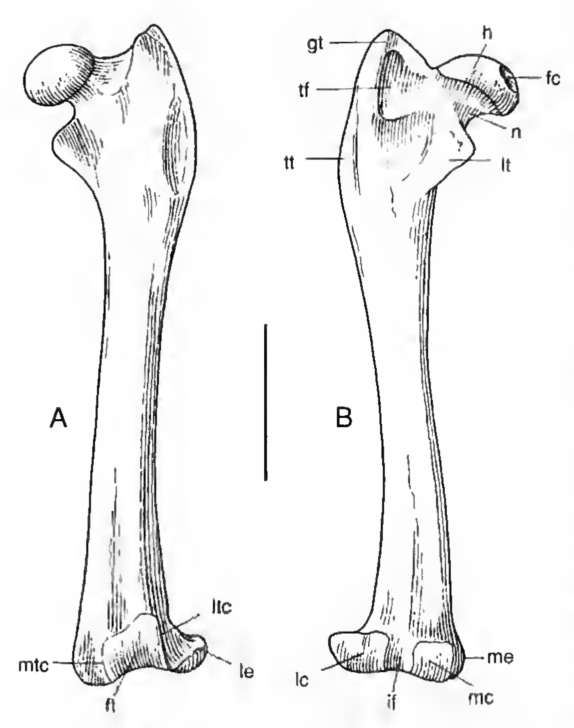


Fig. 33. — *Mayulestes ferox*, holotype (MHNC 1249). Left femur: **A**, anterior; **B**, posterior. Abbreviations: **fc**, fovea capitis; **ft**, femoral trochlea; **gt**, greater trochanter; **h**, head; **if**, intercondylar fossa; **lc**, lateral condyle; **le**, lateral epicondyle; **lt**, lesser trochanter; **ltc**, lateral trochlear crest; **mc**, medial condyle; **me**, medial epicondyle; **mtc**, medial trochlear crest; **n**, neck; **tf**, trochanteric fossa; **tt**, third trochanter. Scale bar: 1 cm.

living genera of the family. In *Caluromys* and *Pucadelphys* it is extremely flat as in *Mayulestes* but more salient.

In ventrolateral view, the dorsal borders of the ilium and the ischium of *Mayulestes* make an angle of approximately 155°. In didelphids, phalangerids, *Cladosictis*, *Prothylacynus* and *Thylacinus* the dorsal borders of the ilium and the ischium are roughly parallel and aligned.

Femur. (Figs 32, 33) Neither of the femora of the holotype of *Mayulestes* is complete. The left femur is the best preserved but lacks a small portion of the neck, the apex of the lesser trochanter, part of the diaphysis and the medial distal condyle; furthermore, the distal part of the shaft shows a slight post-mortem deformation. The right femur lacks the apex of the greater trochanter, the distal third of the diaphysis and a small posterior portion of the medial distal condyle. Both bones, however, allow an accurate reconstruction of the femur of *Mayulestes*.

The femur of *Mayulestes* is relatively short when compared to those of *Cladosictis* and *Prothylacynus* but resembles that of *Borhyaena* which is more massive. It is shorter than that of *Caluromys* but its proportions are close to that of *Didelphis*. In lateral view, the proximal epiphysis is clearly bent anteriorly as in *Cladosictis*, *Pucadelphys* (Fig. 34) and *Caluromys*, contrary to *Borhyaena* where it is almost straight. In *Didelphis* and *Thylacinus*, the curvature is present but much less pronounced than in *Mayulestes*. That feature is also very clear in proximal view. The proximal condyle (or head) is slightly elongated in proximomedial view (*i.e.* compressed anteroposteriorly) and the articular surface extends on the neck laterally (there is a small variation between both femora since the condyle of the right femur is slightly more compressed anteroposteriorly). This condition is relatively similar to that of *Caluromys*, *Didelphis* and the other borhyaenoids. However, the proximal condyle of *Mayulestes* is less globular than in these forms and more resembles in this respect that of *Thylacinus*. The fovea capitis for the attachment of the ligament of the head of the femur is located on the posteromedial side of the head, close to the border of the articular surface. It differs from what is observed in *Didelphis*,

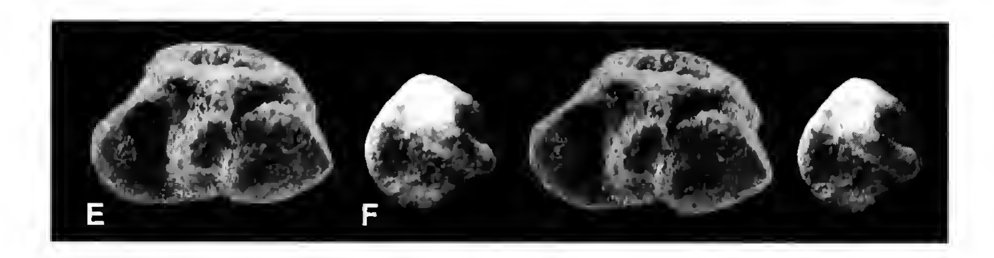
Caluromys and *Cladosictis*, where it is somewhat more central on the condyle; it is closer to the position observed in *Borhyaena* and *Thylacinus*. The fovea capitis is larger than in didelphids and other borhyaenoids, suggesting a much stronger attachment of the ligament in *Mayulestes*. The neck is short as in *Caluromys* and differs from that of *Cladosictis* and, to a lesser extent, *Didelphis*, which are longer. In this respect, it somehow resembles those of *Borhyaena* and *Prothylacynus*. The head and the neck are oriented less proximally and the distal side of the neck is more concave than in *Cladosictis* and *Didelphis* but they resemble the condition observed in *Caluromys*. The greater trochanter is for the insertion of the three glutei, two of which have their origin on the lateral side of the ilium. The gluteus medius is inserted on the posteroproximal angle, and the gluteus profundus on the anteroproximal angle. The greater trochanter of *Mayulestes* is higher than the condyle, a condition also found to a lesser extent in *Borhyaena* and *Thylacinus*. In *Cladosictis*, *Prothylacynus*, *Didelphis* and *Caluromys* the greater trochanter is always lower than the condyle. In lateral view, the greater trochanter has an angular apex with salient insertion areas for the glutei medius and profundus. On the anterior side of the greater trochanter is an elongated shallow fossa, for the vasti lateralis and intermedius, which runs distally along approximately one quarter of the length of the bone. That fossa is absent in *Cladosictis*, *Prothylacynus*, *Thylacinus*, *Caluromys* and *Didelphis*; in *Borhyaena* the origin of the vasti lateralis and intermedius is a slightly depressed area located on the anterior side of the greater trochanter. The lesser trochanter is a large medial triangular blade on the apex of which is inserted the tendon of the iliopsoas (iliacus + psoas major). It is clearly more developed than in *Prothylacynus*, *Cladosictis*, *Borhyaena* and *Thylacinus*. It resembles those of *Didelphis* and *Caluromys*, although larger and thinner. Distal to the greater trochanter, on the lateral side of the bone, is the third trochanter. In fact, in *Mayulestes*, it is more a lateral expansion of the bone than a trochanter, which is in continuity with the anterolateral crest of the greater trochanter. The third trochanter receives the insertion of the glureus superficialis, an important abductor and inverter of the hip. In *Mayulestes*, the area of the third trochanter is markedly expanded laterally while it is straight in *Cladosictis*, *Prothylacynus*,



Fig. 34. — *Pucadelphys andinus* (YPFB Pal 6106). Right femur: **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial; **E**, proximal; **F**, distal views. Scale bar: 5 mm.



Fig. 35. — *Mayulestes ferox*, holotype (MHNC 1249). Right tibia: **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial; **E**, proximal; **F**, distal views. Scale bar: A-D, 1 cm; E, F, 5 mm



Borhyaena and *Thylacinus*. In *Didelphis*, posteromedial to the insertion of the gluteus superficialis and laterodistal to the apex of the lesser trochanter is a small tubercle for the insertion of the quadratus femoris, an extensor of the hip and an evertor of the thigh. No such tubercle exists on the holotype of *Mayulestes*, while it is strongly developed in *Cladosictis*, *Prothylacynus*, *Borhyaena* and *Thylacinus*. In *Cladosictis* it is especially salient and connected to the lesser trochanter proximomedially through an oblique ridge. On the posterior side of the greater trochanter, the trochanteric fossa receives the obturatorii internus and externus and the gemelli muscles. The fossa is deep but not very elongated proximodistally. Its distal extremity is slightly more proximal than the level of the apex of the lesser trochanter. This condition differs from those of *Cladosictis*, *Prothylacynus*, *Borhyaena* and *Thylacinus*, where the fossa is much longer and reaches the distal extremity of the lesser trochanter blade distally. The trochanteric fossa of *Mayulestes* is much more reduced than in these genera and resembles those of *Didelphis* and *Caluromys*. In lateral view of the bone the shaft is straight as in didelphids and the Santa Cruz borhyaenoids. It differs from *Thylacinus* whose femur is bent posteriorly, a cursorial feature.

The anterior face of the distal extremity of the femur bears a large trochlea (the patella was probably absent in *Mayulestes*) for the passage of the tendons of the vasti and rectus femoris muscles. It is deep when compared to didelphids and has an important proximal extension on the anterior side of the shaft; the extension of the trochlea is more developed on the lateral side than on the medial. The trochlea is shifted laterally, approaching the condition of *Eozostrodon* (Jenkins & Parrington 1976). The lateral and medial borders of the trochlea form sharp crests, the lateral one being more elevated than the medial one. The trochlea of *Mayulestes* is more developed than in the other borhyaenoids: it is wider, has more pronounced relief and expands more distally on the shaft. It is, however, closer to that of *Cladosictis* than to those of *Borhyaena* and *Prothylacynus*, although it is wider. It differs from that of *Didelphis* which has a less pronounced relief, and is notably different from that of *Caluromys*, which is distoproximally very short and very flat. The distal extremity of the shaft, proximal to the trochlea, bears a shallow sulcus for the passage of the tendon of the vasti and rectus femoris. A similar condition is observed in *Thylacinus*. In the other borhyaenoids and in *Didelphis* there is no groove but a flat surface which also corresponds to the passage of the tendon. That region of the femur in *Caluromys* is slightly convex.

In distal view, the lateral condyle is conspicuously larger and wider than the medial. This condition is close to that of *Didelphis*, *Caluromys* and *Phalanger* where the medial condyle is narrower than the lateral (although more pronounced in these genera), but differs from that observed in *Cladosictis*, *Borhyaena* and *Prothylacynus*, where the lateral condyle is narrower than or subequal to the medial one. Since the medial condyle of *Mayulestes* is not completely preserved, it is not possible to observe the relative anteroposterior extension of both condyles. However, it is probable that the medial condyle was at least as long as the lateral one or even slightly longer. In lateral view it is noteworthy that the lateral condyle is much less globular than in *Cladosictis*, *Prothylacynus*, *Didelphis* and *Caluromys*. The articular surface of the lateral femoral condyle of *Mayulestes* is not recurved posteroproximally as in these genera and the condyle is protruding posteriorly, a condition that must have reduced the

amplitude of the movement posteriorly (the flexion of the knee). There is a large and deep postcondylar fossa [called popliteal surface by Evans & Christensen (1979) in the dog], probably a consequence of the little recurved posterior border of the condyles. In anterior or posterior view, the medial condyle is slightly lower (*i.e.* more distal) than the lateral one as in *Prothylacynus*, *Cladosictis*, *Borhyaena*, *Thylacinus*, *Didelphis* and *Caluromys*. On the lateral side of the lateral condyle is the fossa for the origin of the popliteus muscle (which logically should be called popliteus fossa). It is small and shallow as in *Didelphis* and *Caluromys* but differs from *Cladosictis*, *Prothylacynus*, *Borhyaena* and *Thylacinus* where it is well marked. The epicondyles are not significantly different from those of the genera considered here. In distal view, the distal epiphysis of the femur is less flattened anteroposteriorly than in *Didelphis*, *Caluromys*, *Monodelphis* and *Philander* but approaches the condition of *Metachirus*. It is however clearly wider than long and approaches the condition observed in the Santa Cruz bothyaenoids; it is proportionally slightly longer anteroposteriorly than in *Prothylacynus* and *Borhyaena* but slightly shorter than in *Cladosictis*.

Patella. No patella has been found associated to the holotype and it is suggested that it was not ossified in *Mayulestes* as it generally occurs in didelphids.

Tibia. (Figs 35, 36) The bone has the typical didelphid sigmoid shape, a condition that is found in all the representatives of the family. In *Mayulestes* it is more pronounced than in *Didelphis* and *Caluromys*; less marked than in *Chironectes* but similar to what is observed in *Marmosa* and *Lutreolina*. In *Prothylacynus* and *Thylacinus* the tibia is straight and, in *Cladosictis*, its distal extremity is slightly bent medially. In *Mayulestes*, in posterior view the proximal third of the shaft is concave laterally and the two distal thirds are convex. The same condition is found in *Didelphis*, *Marmosa* and *Caluromys*; in *Chironectes*, *Metachirus* and *Lutreolina* the inflexion point is located at the middle of the shaft. The tibia of *Thylacinus* is also slightly concavoconvex with the inflexion point at the middle of the shaft. In lateral and distal view, the shaft of the tibia of *Mayulestes* is regularly bent posteriorly as in didelphids, contrary to the condition of the Santa Cruz borhyaenoids.

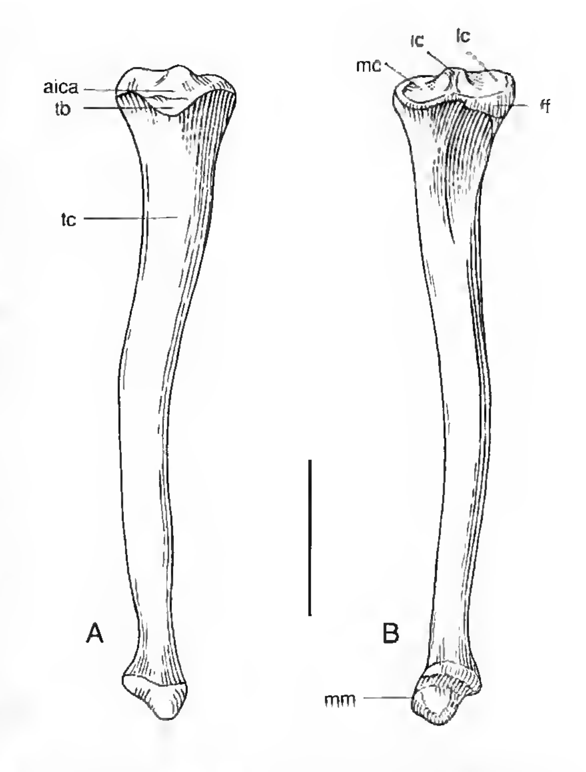


Fig. 36. — *Mayulestes ferox*, holotype (MHNC 1249). Right tibia: **A**, anterior; **B**, posterior views. Abbreviations: **aica**, anterior intercondyloid area; **ff**, fibular facet; **ic**, intercondyloid eminence; **lc**, lateral condyle; **mc**, medial condyle; **mm**, medial malleolus; **tb**, tibial tuberosity; **tc**, tibial crest. Scale bar: 1 cm.

In proximal view, the proximal epiphysis is short anteroposteriorly as in *Caluromys* and *Didelphis* (to a lesser extent in this genus) and differs from the condition observed in *Prothylacynus* and *Cladosictis*, whose proximal epiphysis of the tibia is markedly triangular. The tibial tuberosity is small and very little salient anteriorly. It is smaller than in *Caluromys* and *Didelphis* and much smaller than in *Prothylacynus*, *Cladosictis* and *Thylacinus*, where its development is responsible for the triangular shape of the proximal epiphysis. In lateral view the tibial tuberosity is truncated and forms a regular slope on the anteroproximal angle of the tibia. This condition is found in all didelphids and borhyaenoid but differs from that observed in *Thylacinus* where the tuberosity is very salient and forms a right angle with the shaft. Between the tuberosity and the

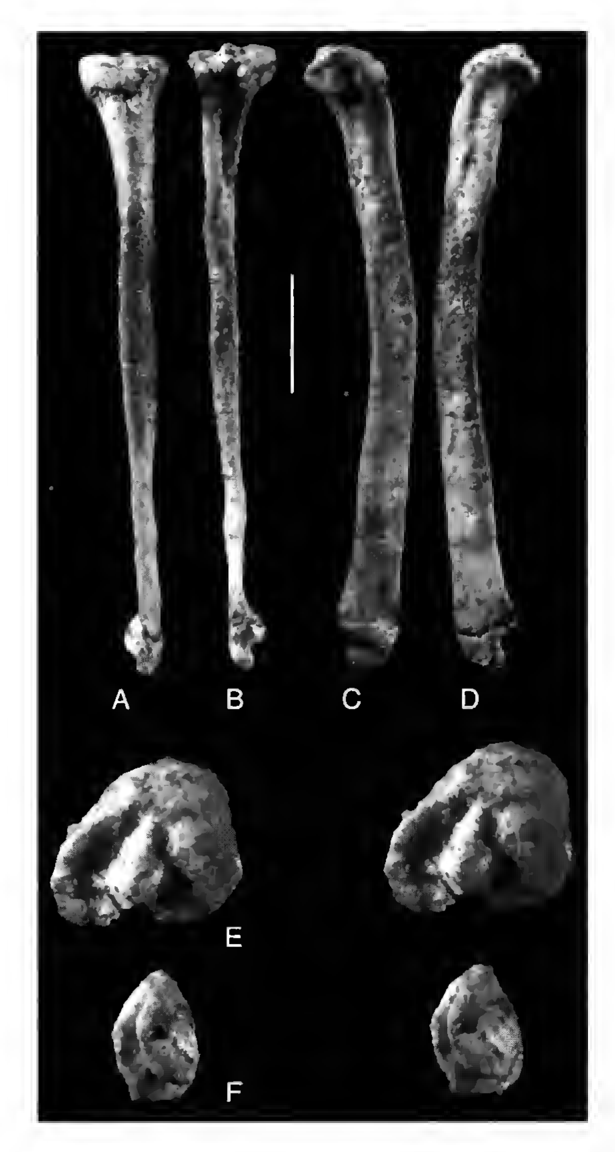


FIG. 37. — *Pucadelphys andinus* (YPFB Pal 6106). Right tibia: **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial; **E**, proximal; **F**, distal views. Scale bar: A-D, 5 mm; E, F, 2.5 mm.

condyles is a surface of rugose bone called the anterior intercondyloid area. This area is very short anteroposteriorly as in *Caluromys* and *Didelphis* and differ from the very long area observed in *Prothylacy-nus, Cladosictis* and *Thylacinus*. The lateral tibial condyle is subtriangular, almost flat; the medial condyle is reniform, excavated and is a little more distal than the lateral. The two condyles are anteroposteriorly shorter than in *Caluromys, Didelphis Thylacinus* and probably *Cladosictis* (the two specimens I could observe during this study had a poorly preserved proximal extremity). In *Prothylacynus* the condyles are even shorter than in *Mayulestes* and the medial condyle is subcircular in shape. The fibular facet of *Mayulestes* is elongated transversely and has a posterolateral orientation as in all didelphids and borhyaenoids observed during this study. The intercondyloid eminence is well-developed and rounded. It is larger than in *Prothylacynus* but smaller than in the didelphids and *Thylacinus*. The posterior intercondyloid area is almost absent and corresponds to the posterior slope of the intercondyloid eminence. There is a small posterior intercondyloid area in *Prothylacynus, Cladosictis* and *Thylacinus*.

On the anterior edge of the proximal extremity of the shaft is an unatural ovoid cavity. It is difficult to determine if this structure is pre-mortem (*i.e.* pathological or traumatological) or post-mortem (*i.e.* taphonomical), although the smoothness of its edges would indicate some bone growth and would favour the pathological-traumatological hypothesis.

The tibial crest is smoothly convex and does not form a rounded keel as in *Caluromys, Didelphis, Prothylacynus* and *Cladosictis*. The keel is much more salient and much narrower in *Thylacinus*. The lateral tibial fossa is small but well marked. It is smaller than in *Prothylacynus* and *Thylacinus* but deeper than and not as flat as in *Didelphis* and *Caluromys*. The medial tibial fossa is well-developed as in *Caluromys* and differs from the condition observed in *Prothylacynus, Cladosictis, Thylacinus* and *Didelphis*, where it is more a flat area than a fossa. On the posterior side of the proximal extremity of the shaft is a deep fossa located distal to the popliteal notch. As it stands in *Mayulestes*, it is probable that it has been emphasised by a post-mortem deformation. However, it seems to have been relatively deeper than in the didelphids, a condition similar to that observed in *Prothylacynus* and *Cladosictis*. The distal two thirds of the shaft are transversely compressed as in *Prothylacynus, Cladosictis* and *Thylacinus*. This condition is also found in *Caluromys* and *Didelphis*, where it is more pronounced. On the posterolateral side of

the shaft is a marked crest running distally from the posterior tibial fossa toward the distal extremity until the distal third of the bone. This crest is probably for the interosseous membrane which unites the tibia and fibula as in all didelphids. This structure is stronger than in *Prothylacynus* but it is much weaker than in *Cladosictis* where it almost reaches the distal extremity of the shaft.

The distal extremity bears the articular surface for the astragalus which is divided into a medial and a lateral facet. In *Mayulestes* both facets form a marked angle a little larger than 90°. It resembles the condition of *Prothylacynus* and *Cladosictis*, where the angle is close to 90° (or slightly smaller) and differs from the condition observed in the living didelphids where the angle is much more open. The malleolus is large and high and occupies the entire length of the anteromedial side of the distal epiphysis, contrary to the didelphid condition where the malleolus is anteroposteriorly shorter. The condition of this feature in *Cladosictis* is intermediate between those of *Mayulestes* and didelphids. The malleolus is flattened transversely and its major axis has a posteromedial-anterolateral orientation and forms an angle of approximately 48° with the transverse axis of the tibial condyles. In the Santa Cruz borhyaenoids and in *Thylacinus*, the plane of the malleolus is at 90° with the transverse axis of the femorotibial articulation (the functional interpretation and significance of this feature are discussed below). The medial facet of the astragalotibial articulation is large as in the other borhyaenoids, unlike in didelphids, where it is short, anteroposteriorly and proximodistally. It is strongly convex and faces posterolaterally. The lateral facet of the articulation is reniform, slightly concave and oriented slightly obliquely in relation to the boundary (in lateral view) between the epiphysis and the shaft (Fig. 35C). This condition is intermediate between that of *Prothylacynus* and *Thylacinus*, where it is parallel, and that of didelphids, where the facet always makes an angle of 30 to 45° with the limit between the epiphysis and the shaft. As a consequence, the lateral astragalotibial facet of didelphids is helical and screws around the malleolus. The astragalotibial articulation of *Cladosictis* is also slightly oblique as in *Mayulestes* but its astragalotibial articulation is not helical as in the didelphids. The lateral facet is short anteroposteriorly as in *Prothylacynus* and *Thylacinus* and differs from those of *Cladosictis* and *Didelphis* which are longer. In *Pucadelphys* the condition of the distal articulation of the tibia is similar to that of *Mayulestes* (Fig. 37). The malleolus forms an angle of approximately 69° with the axis of the femorotibial articulation and the lateral and medial facets of the astragalotibial articulation are approximately at right angle.

The articular facet for the fibula is located on the lateral edge of the distal epiphysis. In *Mayulestes*, it is shorter proximodistally than in *Prothylacynus* and *Cladosictis* and occupies the whole posterolateral edge of the distal epiphysis. It differs from that of *Thylacinus* where it is restricted to the anterolateral angle of the epiphysis. As in *Prothylacynus* and *Cladosictis*, the lateral edge of the distal epiphysis is more salient than in *Thylacinus* and in didelphids (where it is almost in continuity with the lateral side of the shaft).

Fibula. (Fig. 38) Only the distal extremity of the right fibula is known. The distal epiphysis has a subtriangular shape in distal view. Contrary to what is observed in didelphids, it is very salient medially and it is probable that the distal extremity of the shafts of the bones were broadly separated. The articular surface for the astragalus is concavoconvex; it is not possible to observe whether it was articulating also with the calca-

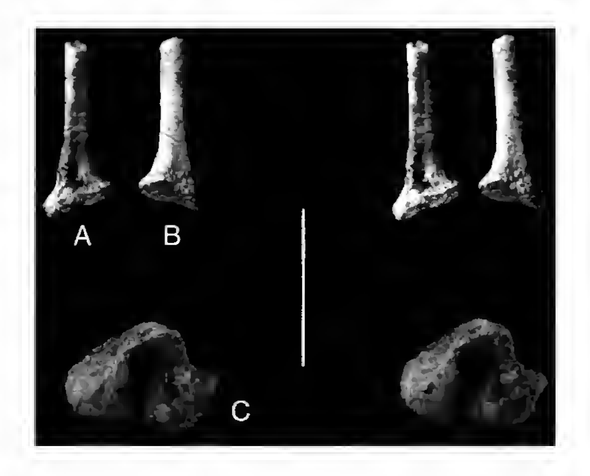


Fig. 38. — *Mayulestes ferox*, holotype (MHNC 1249). Right fibula: **A**, anterior; **B**, posterior; **C**, distal views. Scale bar: A, B, 1 cm; C, 5 mm.

neum or not. In the didelphids, there is no fibulocalcanear articulation, except in *Didelphis*, *Metachirus* and *Chironectes* (Szalay 1994: 196, 340). On the lateral side of the epiphysis is a well marked groove for the passage of the tendon of the extensor digitorum lateralis and peroneus brevis and longus muscles. A similar condition is found in the living didelphids. In *Prothylacynus* and *Cladosictis*, the passage of the tendon is a flat area and there is no groove.

Tarsus. (Figs 39, 40) The calcaneum is the only bone of the tarsus that is known in *Mayulestes*. The right calcaneum is complete; only the distal extremity of the left one is preserved. Comparisons of that bone will be made with those of *Sipalocyon* (YPM PU 15154), *Cladosictis* (YPM PU 15046) and with six large (for the fauna) calcanea from the early late Palaeocene of Itaboraí (Brazil) which are most likely referable to borhyaenoids although not necessarily to the same taxon. Because of their size, the four smaller specimens (DGM 1. 175-M, 176-M, 178-M, 179-M) belong to the IMG (Itaboraí Metatherian Group) XI of Szalay (1994) and could fit the genus *Patene* while the two larger ones (DGM 1. 180-M, 184-M) belong to the IMG XIII of Szalay (1994) and could fit *Nemolestes*. In the following description, for practical reasons they will be referred to the "Itaboraí borhyaenoid calcanea" and no reference is made to specific genera.

The tuber calcanei of *Mayulestes* is relatively lon-

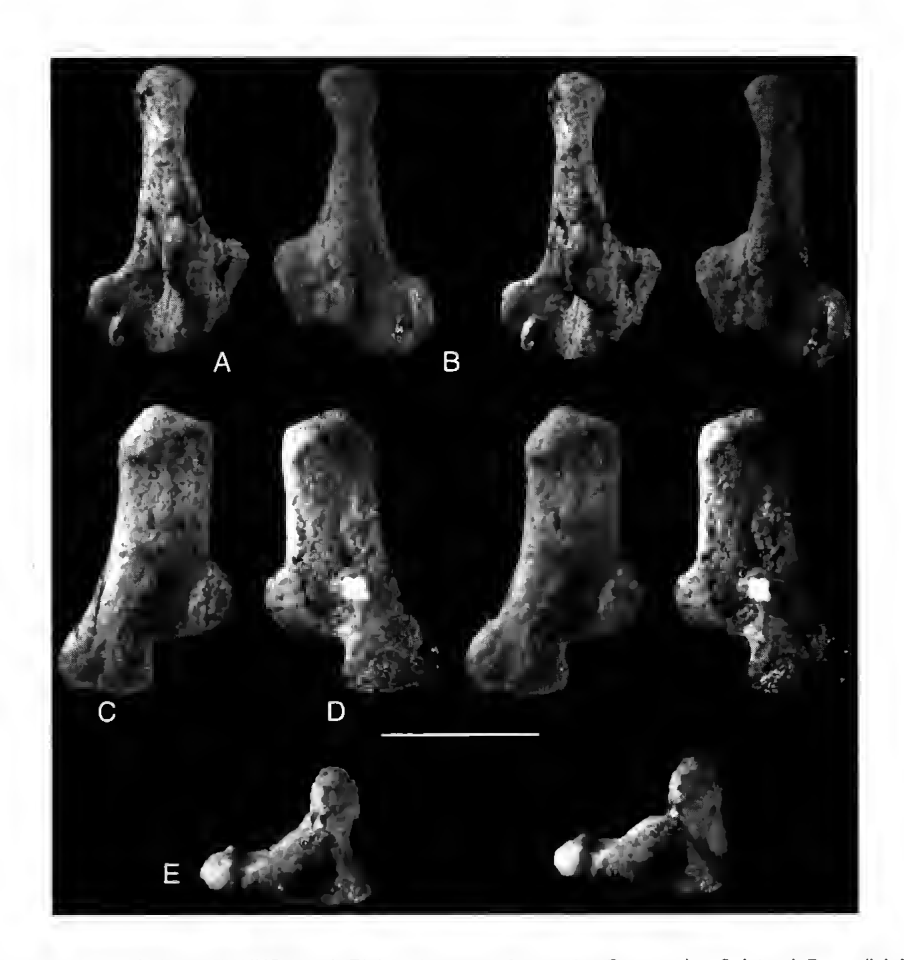


Fig. 39. — *Mayulestes ferox*, holotype (MHNC 1249). Right calcaneum: **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial; **E**, distal views. Scale bar: 5 mm.

ger and more slender than in *Cladosictis*, *Sipalocyon* and the Itaboraian calcanea. The ectal facet (the lateral articular facet for the astragalus) is small, short proximodistally and very narrow. Lateral to the ectal facet there was either no calcaneofibular (CaFi) facet or a very narrow strip-like facet. A calcaneofibular facet is present in *Cladosictis* and *Sipalocyon* and in all the Itaboraí borhyaenoid calcanea mentioned above. In one specimen figured by Szalay (1994, fig. 6.27 A-C), the calcaneofibular facet is very similar to that which could exist in *Mayulestes* in its length, narrowness and orientation, while in the other specimens the facet is generally wider and/or obliquely oriented. In the Itaboraí borhyaenoid calcanea, the articular contact with the fibula is generally smaller than in *Cladosictis* and *Sipalocyon* (Szalay 1994, fig. 6.27, 6.31), although it is larger (as large as the ectal facet) in DGM 1.160-M, a specimen which "falls within the range expected for *Patene*" (Szalay 1994: 177). On the lateral side of the protuberance which bears the ectal and fibular facets is a well marked insertion area for the calcaneofibular ligament. Medially, the dorsal side of the sustentaculum tali bears the sustentacular facet (the medial articulation for the astragalus). It is smaller and more gracile than in *Cladosictis* and *Sipalocyon* and, as in these genera, its articular facet occupies the entire length of its dorsal side and reaches distally the dorsolateral edge of the cuboid facet, contrary to the condition observed in didelphids. The sustentacular facet is slightly oblique relatively to the axis of the tuber calcanei as observed in the Itaboraí calcanea and *Sipalocyon*, contrary to the condition of *Cladosictis*, where it is parallel to the tuber. The orientation of the plane of the sustentacular facet is mainly medial with a small dorsal component. In *Sipalocyon* its orienration is almost totally dorsal and in didelphids it is intermediate between *Mayulestes* and *Sipalocyon*. The peroneal process of the calcaneum is expanded distolaterally and bears a deep groove for the passage of the peroneus longus. In *Mayulestes* the peroneal process is larger and the groove is deeper than in *Cladosictis* and *Sipalocyon*; in these respects, they are similar to those of the Itaboraí calcanea. Furthermore, the lateral wall of the sulcus is very thick and longer than the medial in *Mayulestes* as in the Itaboraí calcanea, contrary to *Cladosictis* and *Sipalocyon*. The large and laterally expanded peroneal process of *Mayulestes* leaves a large space for the passage of the tendon of the peroneus brevis on its anterior face, and for the abductor digiti quinti on its posterior face (Godinot & Prasad 1994; Prasad & Godinot 1994). The posterior face of the calcaneum of *Mayulestes* possess a small ridge which runs distally from the postemedial edge of the tuber calcanei and reaches the small distal plantar tubercle on the posterior border of the calcaneocuboid articulation. The posterior side of the peroneal process is wide and deeply concave and that of the sustentaculum tali is relatively flat. In *Sipalocyon* and *Cladosictis*, the ridge is much more developed than in

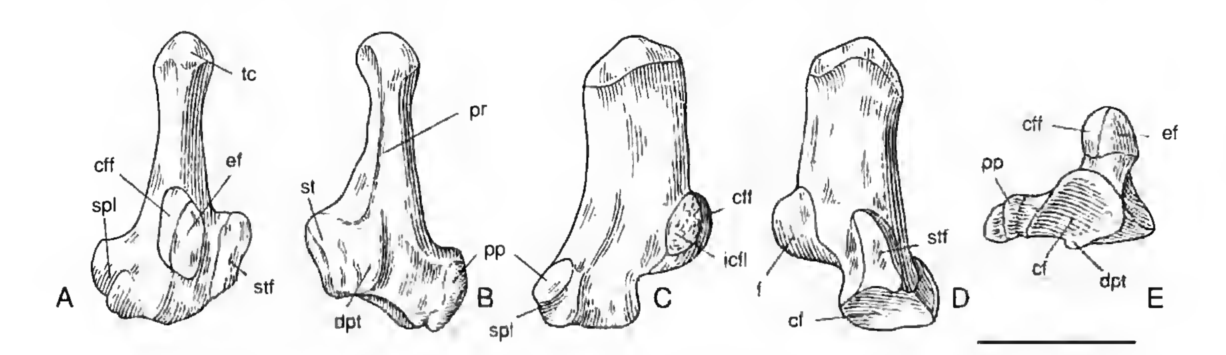


FIG. 40. — *Mayulestes ferox*, holotype (MHNC 1249). Right calcaneum: **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial, **E**, distal views. Abbreviations: **at**, anterior plantar tubercle; **cf**, cuboid facet; **cff**, calcaneofibular facet; **dpt**, distal plantar tubercle; **ef**, ectal facet; **icfl**, insertion for calcaneofibular ligament; **pp**, peroneal process; **pr**, posterior ridge; **spl**, sulcus for the passage of the peroneus longus; **st**, sustentaculum tali; **stf**, sustentacular facet; **tc**, tuber calcanei. Scale bar: 5 mm.

Mayulestes, the posterior side of the sustentaculum is convex and the posterior side of the peroneal process is narrow and only slightly concave. When compared to that of *Mayulestes*, the posterior side of the calcaneum of *Sipalocyon* and *Cladosictis* is inflated posteriorly, probably in order to strengthen the bone. In the Itaboraí calcanea, the condition is intermediate between that of *Mayulestes* and those of *Cladosictis* and *Sipalocyon* since they have a slightly thicker posterior ridge. As a consequence of the morphology of the posterior side of the calcaneum, in distal view, the articular facet for the cuboid has a straight border in *Mayulestes*, while it is convex posteriorly in *Cladosictis* and *Sipalocyon*. The condition of the Itaboraí calcanea resembles more that of *Mayulestes* than that of the Santacruzian genera. As in the Itaboraí calcanea, the cuboid facet is deeper in *Mayulestes* than in *Sipalocyon* and *Cladosictis*.

The calcaneum of *Mayulestes* differs from that of *Didelphis* which is more specialised. In *Didelphis* the tuber calcanei is more robust and short, the ectal facet is very narrow, the sustentacular facet does not reach the cuboid facet distally, and the sustentaculum tali is notched medially. The sustentacular and ectal facets are very close to one another in *Didelphis*, while they are well separated in *Mayulestes*, the peroneal process is small, does not reach the lateral border of the cuboid facet distally, and the groove for the peroneal muscle has lost its medial wall. Furthermore, the calcaneum of *Mayulestes* differs from that of most didelphids [a secondarily acquired CaFi facet is present in *Didelphis* (although small in this genus), *Metchirus*, and *Chironectes* (Szalay, 1994)] which have lost the calcaneofibular (CaFi) facet, a derived condition also found in peradectids (Szalay 1994). Contrary to the statement by Marshall & Sigogneau-Russell (1995), the calcaneum of *Pucadelphys* has a clear calcaneofibular facet distinctly observable on the further prepared left tarsus of YPFB Pal 6106 (Fig. 41).

One of the most characteristic modifications of the calcaneum of didelphids is the presence, posteriorly, of a deep notch on the posterior border of the cuboid facet for the articulation of a large proximal styloid process of the cuboid, around which the calcaneum probably has some rotation ability (CaCup facet of Szalay 1994). Both cuboid (Cacud and CaCup) facets are separated by a well marked semicircular ridge. This feature, which is a didelphid synapomorphy (Szalay 1994), is absent in *Mayulestes*. Contrary to the statement by Marshall & Sigogneau-Russell (1995: 148), the calcaneum of *Pucadelphys* does not show, even incipiently, any trace of the very typical proximal indentation of the cuboid facet, as it is observed in the living didelphids and in two fossil didelphids from the Palaeocene of

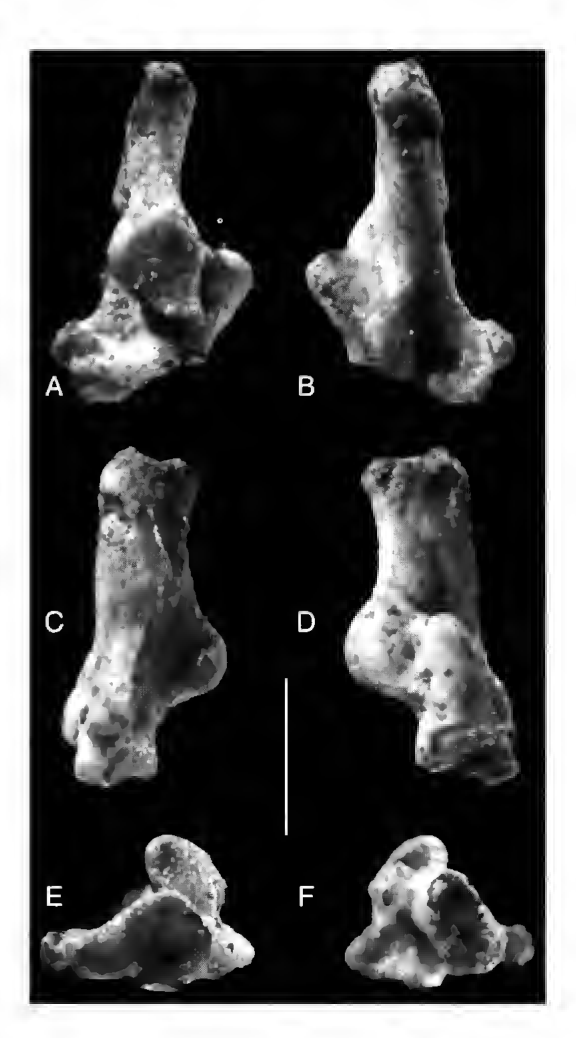


Fig. 41. — *Pucadelphys andinus* (YPFB Pal 6106). Right calcaneum: **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial; **E**, distal; **F**, proximal views. Scale bar: 2.5 mm.

Itaboraí (Brazil) (Szalay 1994, fig. 6.23). In this respect, the calcaneum of *Pucadelphys* is similar to that of *Mayulestes* and to most North American Late Cretaceous and Tertiary marsupial calcanea figured by Szalay (1994: Chapter 6). The calcaneum of *Pucadelphys* does not possess a CaCup facet. In fact, the concavity of the plantar aspect of the cuboid facet (what Marshall & Sigogneau-Russell questionably regard as an incipient development of the didelphid condition) is more pronounced in *Mayulestes* than in *Pucadelphys* (YPFB Pal 6105 and 6106). The specimen YPFB Pal 6110 (Marshall & Sigogneau-Russell 1995, fig. 50) is that of a juvenile and the posterior border of the cuboid facet is probably slightly worn (this has been pointed out to me by D. Sigogneau-Russell). The consequence is that the proximal extension of the cuboid facet of that specimen appears more developed than it actually was, and more than in the other specimens (YPFB Pal 6105 and 6106). Whatever the orientation of the calcaneocuboid facet of *Pucadelphys* is, it is clear that it is simple (*i.e.* it does not have a CaCup facet) and does not present an incipient development of the calcaneocuboid didelphid synapomorphy. Therefore, the calcaneum of *Pucadelphys* does not have two of the major calcanear synapomorphies found in didelphids (presence of CaCup and loss of CaFi facets).

Metatarsus. (Fig. 42) Two metapodials are referred to left MtIII and MtIV. However, the determination of the MtIII is uncertain since part of the proximal extremity is lacking. The relative length and proportions of the MtIII are similar to those of *Sipalocyon* and *Cladosictis*. It is clearly shorter than in *Prothylacynus*. In anterior view, the articular facet for the ectocuneiform is more convex and more bent anteriorly than in *Sipalocyon* allowing probably better flexion movements of the foot. On the distal extremity, the condyle is less globular than in *Sipalocyon* and there is a deep articular fossa on the anterior side of the bone, proximal to the articular condyle. This latter condition also denotes better articulation and wider movement of the digits.

The MtIV is relatively shorter than in *Sipalocyon* and does not present the weak lateral curvature observed in this genus. Its proximal articular facet with the cuboid is more inclined anteriorly and laterally than in *Cladosictis* and would also indicates more agility in the movements of the foot. The distal articulation is similar to that of the MtIII.

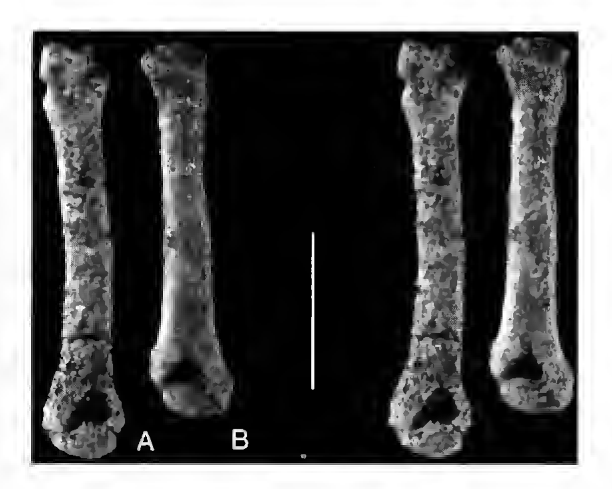


Fig. 42. — *Mayulestes ferox*, holotype (MHNC 1249). **A**, Left MtIII in dorsal view; **B**, Left MtIV in dorsal view. Scale bar: 5 mm.

MtIII (13 mm) is slightly longer than MtIV (12.2 mm). They are both slightly longer than one third of the length of the tibia.

DISCUSSION

Cranial characters

Teeth

Incisors. The number of incisors of *Mayulestes* (I5/i4) is obviously plesiomorphic when compared to that of the other borhyaenoids (I4/i3). Before the discovery of *Mayulestes*, the reduction of the incisors number to I4/i3 was regarded as diagnostic of the Borhyaenoidea (Marshall & Kielan-Jaworowska 1992). Among marsupials, an incisor formula of I5/i4, which is always present in didelphids, is regarded as plesiomorphic. However, Winge (1941) has noted that the I1 was not occluding with any lower incisor and suggested that the i1 had been lost in marsupials. Therefore, the first lower incisor is the i2. Hershkovitz (1982: 186) agrees with this interpretation which is supported by strong embryological evidence (Woodward 1893; Berkovitz

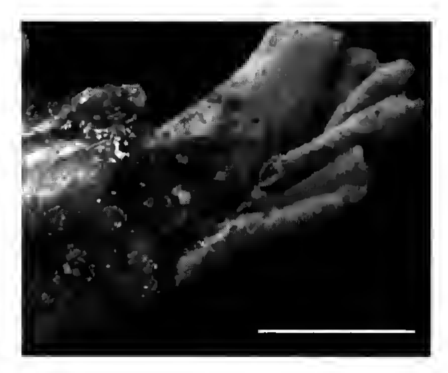



FIG. 43. — Dorsomedial view of the dissected anterior region of a mandible of *Pucadelphys andinus* (YPFB Pal 6473) showing the staggered i3. Scale bar: 2.5 mm.

1978). So far, no marsupials have been found with a complete incisor formula and the plesiomorphic incisor formula for marsupials is that of *Mayulestes*: I5/i4.

Mayulestes has a staggered i3 (*i.e.* second lower incisor). Hershkovitz (1982) has shown that the second lower incisor (i3) of most polyprotodont marsupials has a root which is shifted (staggered) posteriorly and dorsally. Consequently, the anterior alveolar border of the i3 on the dentary is thickened or buttressed. According to Hershkovitz, that feature is present in didelphids, borhyaenoids, several dasyurids, *Thylacinus*, several peramelids and an Early Cretaceous portion of left mandible (FMNH PM583, Theria *incertae sedis*) interpreted (by Hershkovitz) as a metatherian. Contrary to the statement by Marshall & Muizon (1995: 68), the i3 of *Pucadelphys* is actually staggered, as shown by specimens YPFB Pal 6473 and 6474 (Fig. 43). The staggered condition could not be observed in *Pediomys* because of the state of preservation of the specimens. The staggered i3 is absent in the Microbiotheriidae and is not observable in other South American families where hyperspecialisation of the muzzle hides that condition (Caenolestidae, Groeberiidae, Argyrolagidae Peramelidae, and Myrmecobiidae). Among Late Cretaceous taxa, the i3 is apparently not staggered in *Alphadon*, *Kokopellia*, *Eodelphis browni* (AMNH 14149) and *Didelphodon* (USNM 2136); (Cifelli & Muizon 1997, 1998). The staggered i3 has been regarded as a synapomorphy of marsupials (Hershkovitz 1982), but Muizon *et al.* (1997) tentatively regard this character as a synapomorphy of the southern radiation of marsupials (South America and Australia). The microbiotheriid condition must hence be regarded as a reversal.

The upper incisor row of *Mayulestes* is deeply arched posteriorly as in didelphids. In the other borhyaenoids, where that part of the skull is known, the upper incisor row is almost straight and transverse (in *Pharsophorus*, *Sipalocyon*, *Cladosictis*, *Borhyaena*, *Prothylacynus*, *Acrocyon*). A straight upper incisor row is a derived condition within the Borhyaenoidea and the arched upper incisor row of *Mayulestes* is a plesiomorphic condition for the superfamily.

Premolars. The first upper and lower premolars of *Mayulestes* are slightly obliquely set in the maxilla and dentary as it is observed to a much greater extent in the Borhyaeninae and the Proborhyaenidae. The Prothylacininae have a p1 strongly oblique in the dentary but P1 is apparently not oblique. Marshall *et al.* (1990) have regarded the oblique implantation of p1 as a synapomorphy of the Borhyaenidae. However, the presence of this feature in the Proborhyaenidae (*Paraborhyaena*) introduces a contradiction in the cladogram of Marshall *et al.* (1990, fig. 2), as does the presence of an oblique P1 in the Borhyaeninae and the Proborhyaenidae. In fact, node 24 (Borhyaenidae) of Marshall *et al.* (1990, fig. 2) is relatively weakly supported since the other synapomorphy they use to diagnose the family is "animals of medium to large size". The presence of slightly oblique upper and lower first premolar in

Mayulestes would suggest that this is the plesiomorphic condition within the Borhyaenoidea and that it could represent a synapomorphy of the superfamily. The loss of the obliquity in some taxa would therefore have to be regarded as an apomorphic character state related to a lengthening of the tooth row (*Cladosictis*, *Sipalocyon*). However, it is noteworthy that the obliquity of the first lower premolar in the Borhyaenidae and Proborhyaenidae is much more pronounced than in *Mayulestes* and probably also represents an apomorphic trend related to the acquisition of a very short and stout rostrum.

Molars. The molars of *Mayulestes* show a slight increase in size from M1 to M3 and from m1 to m4. In fact, the last lower molar of *Mayulestes* is subequal in height and volume to m3 and only very slightly longer than m3 (length m3 = 3.70, length m4 = 3.74). The character state "trend for molars to increase rapidly from m1 to m4 and from M1 to M3" has been regarded by Marshall & Kielan-Jaworowska (1992) as a synapomorphy of the Borhyaenoidea. However, it is noteworthy that an increase in size from m1 to m4 and from M1 to M3 is also found in the Stagodontidae and in the Dasyuroidea (*Thylacinus*, *Sarcophilus*). In the Creodonta the last lower molar is frequently the largest of the tooth row (*Hyaenodon*, *Pterodon*, *Dissopsalis*, *Quercytherium*, *Cynohyaenodon*). This is also true in several felids and hyaenids. In fact, the tendency to increase the size of the last lower molar and penultimate upper molar is a highly homoplastic character state related to hypercarnivorous diet. Whatever the function is (shearing, crushing or both), the greatest force is located at the posteriormost end of the tooth row (the closest possible to the rotation axis of the condyle), which is probably related to the tendency of various groups of mammals to increase the size of the posteriormost lower tooth. Therefore, the phylogenetic value of the character state "rapid increase in size from m1 to m4 and from M1 to M3" is questionable since it is a highly homoplastic feature. Furthermore, a last lower molar slightly larger than, or subequal in size to, the preceding tooth is also present in the Early Cretaceous eutherian *Prokennalestes*, and in some species of *Cimolestes*. Therefore, it is probable that the condition of *Mayulestes* represents the plesiomorphic character state. The same is probably true for *Eodelphis* and *Pariadens*, where the m4 is only very slightly larger than the m3.

The molar morphology of *Mayulestes* is very similar to that of *Allqokirus* from the same locality (Fig. 44). The holotype of *Allqokirus* is an upper molar referred to an M2 or M3 by Marshall & Muizon (1988). The proportions of the holotype of *Allqokirus* (L = 3.25 mm, W = 3.8 mm, L/W = 0.85) clearly differ from those measured on the M2 (L = 3.05, W = 4.34, L/W = 0.7) and M3 (L = 2.8, W = 4.64, L/W = 0.6) of the holotype of *Mayulestes*. Furthermore, the M2-M3 of *Mayulestes* differ from the holotype of *Allqokirus* in having a much larger stylar cusp D, a low crest descending from the stylar cusp D toward the lingual extremity of the metacrista, a metacrista which does not strongly overhang the base of the crown (as it is observed in *Allqokirus*), a straight posterior edge of the tooth

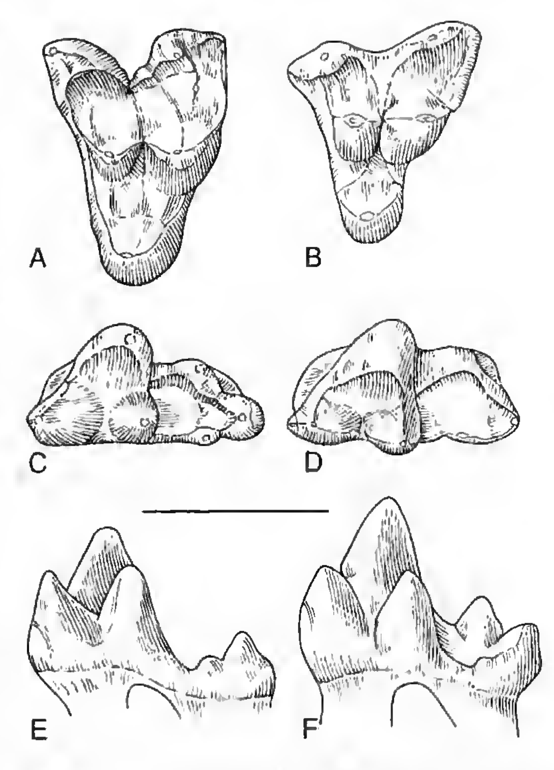


FIG. 44. — Occlusal views of M3 of: **A**, *Mayulestes*; **B**, *Allqokirus*. Occlusal views of m3 of: **C**, *Mayulestes*; **D**, *Allqokirus*. Lingual views of m3 of: **E**, *Mayulestes*; **F**, *Allqokirus*. Scale bar = 2 mm.

(whereas it forms an angle of approximately 150° in *Allqokirus*), a deeper ectoflexus and a more robust and longer protocone. One m3 has been referred to the holotype of *Allqokirus* by Marshall & Muizon (1988). The m3 of *Mayulestes* differs from that of *Allqokirus* in being narrower and more slender. The lower molars of *Mayulestes* resemble those of *Allqokirus* in most of their structure and both are peculiar in having a reduced entoconid and a talonid basin opened anteromedially. The level of morphological similarity existing between *Mayulestes* and *Allqokirus* is similar to that existing between *Cladosictis* and *Sipalocyon*, two different genera found associated in the same localities from the Colhuehuapian and Santacruzian beds of Patagonia.

The borhyaenoid molar morphology shows several evolutionary trends which represent a functional complex related to postvallum-prevallid shear, characteristic of hypercarnivorous adaptation (Muizon & Lange-Badré 1997). On the lower molars, the metaconid reduces and disappears in most genera; the paraconid is enlarged and crest-like, and the paractistid tends to rotate counter-clockwise, being almost parallel to the tooth row in some borhyaenids, some proborhyaenids and in thylacosmilids; the talonid tends to reduce and almost disappears in borhyaenids, proborhyaenids and thylacosmilids. On the upper molars, the paracone and the protocone are always reduced and almost disappear in some borhyaenids, proborhyaenids and thylacosmilids; the stylar shelf and stylar cusps B and D are generally very reduced and often totally disappear; the postmetacrista is greatly enlarged and tends to be aligned with the metacone, parallel to the tooth row. These features are highly adaptive and can be observed (some or all) in five other groups of mammals: Deltatheroida, Stagodontidae, Dasyuroidea (*Thylacinus* and *Sarcophilus*), Creodonta and Carnivora (Muizon 1994; Muizon & Lange-Badré 1997). Therefore the functional complex based on postvallum-prevallid shear is a highly homoplastic synapomorphy with a low phylogenetic value and it should not be retained as a key synapomorphy of the borhyaenoids.

In *Mayulestes*, the molar morphology is relatively unspecialised for a borhyaenoid but some of the features related to postvallum-prevallid shear are already incipiently developed: the paracone is smaller in volume and height than the metacone, the postmetacrista is enlarged, the metaconid is subequal in height to, but smaller in volume than, the paraconid, and the paraconid is slightly blade-like. The same features are also present in *Allqokirus*. The molar morphologies of *Mayulestes* and *Allqokirus* are very similar to that of *Patene*. However, the former genera differ from the latter in the very small size of their entoconid and in the lingual opening of the talonid basin, while in *Patene* the entoconid is subequal in height and volume to the hypoconulid and the talonid basin is not opened lingually. The small size of the entoconid of *Allqokirus* has been regarded as a plesiomorphy within the borhyaenoids by Marshall & Kielan-Jaworowska (1992). A small entoconid is also found in the Deltatheroida and probably in *Aegialodon*; this cusp is absent in *Kielantherium* and *Hypomylos*, two Early Cretaceous tribosphenidans (respectively, Dashzeveg & Kielan-Jaworowska 1984 and Sigogneau-Russell 1992). Marshall & Kielan-Jaworowska may be correct since *Allqokirus* and *Mayulestes* are the oldest known borhyaenoids and since, in younger genera of the superfamily, the entoconid, when present, is always well-developed. However, various lineages of borhyaenoids show a tendency to reduction of the talonid, which is often achieved by the reduction of the entoconid and the lingual opening of the talonid basin [*Plesiofelis schlosseri* (MLP 11-114), *Notogale mitis* (MNHN SAL 97), *Anatherium herrerae* (FMNH 13521), *Chasicostylus castroi* (MLP 57-XI-2), an isolated m1 (MNHN SAL 272) from the Deseadan beds of Salla (Bolivia), probably referable to a small species of *Pharsophorus*]. Therefore, since this feature has appeared several times independently in several groups of borhyaenoids, the reduction of the entoconid of *Mayulestes* and *Allqokirus* may very well have also occurred in the Mayulestidae (*Allqokirus* and *Mayulestes*) and would be, therefore, a synapomorphy of the family. This hypothesis is tentatively retained here. It is noteworthy that the earliest known marsupial genera (*Kokopellia*, from the Albian-Cenomanian of Utah, *Pariadens*, from the Cenomanian of

Utah) have a well-developed entoconid. A similar condition is present in *Asiatherium* from the Late Cretaceous of Mongolia.
The apomorphy of the reduced entoconid of *Allqokirus* has been previously mentioned by Szalay (1994: 321, 328). If this assumption is correct, *Mayulestes* and *Allqokirus* cannot be regarded as probable morphological ancestors for *Patene* (as it was suggested by Marshall & Muizon 1988 and Muizon 1992) but could represent a morphological dental ancestor for a lower molar from the late Palaeocene of Itaborai referred by Marshall (1978) to cf. *Nemolestes* sp. This tooth (a posterior molar, m3 or m4) has a high protoconid, a large crestlike paraconid and a small metaconid cuspule at the posterolingual base of the protoconid. The talonid is very reduced, the talonid basin is open lingually and the entoconid is either extremely reduced or totally absent. The genus *Nemolestes* has been regarded by Marshall (1978) and by Marshall *et al.* (1990) as the oldest known representative of the Borhyaenidae. If these authors are correct, then *Allqokirus* and *Mayulestes* would not be ancestral the Hathlyacinidae as previously stated by Marshall & Muizon (1988) and Muizon (1992) (for *Allqokirus* only) but could represent the sister-group of the Borhyaenidae. However, this hypothesis still has to be tested with the discovery of cranial remains of *Nemolestes*.
The stylar cusps and stylar shelf of the upper molars of *Mayulestes* and *Allqokirus* are well-developed for borhyaenoids. The only other borhyaenoid genus whose upper molars have well-developed stylar shelf and stylar cusps is *Patene*. *Mayulestes* and *Patene* resemble each other in having a stylar shelf larger than in the other borhyaenoids, conspicuous stylar cusps A and B and no cusp in a stylar C position. However, on the M3 of the holotype of *Patene simpsoni* and on an isolated M3 from Itaboraí (DGM uncatalogued specimen), a series of small cuspules are observed in a stylar cusp C position. *Mayulestes* differs from *Patene* in having a larger stylar shelf, a larger stylar cusp B and a conspicuous stylar cusp D (absent in *Patene*). A stylar cusp B is also present in *Procladosictis* from the Mustersan of Patagonia. The stylar cusps and stylar shelf of *Mayulestes* are extremely similar to those of the Stagodontidae (*Eodelphis* and *Didelphodon*) which also have a large stylar shelf with well-developed stylar cusps B and D and which lack a cusp in a stylar cusp C position. However, a series of cuspules in stylar cusp C position, similar to that of *Patene*, is also observed in some specimens of *Eodelphis* and *Didelphodon* (Fox 1981). As in *Mayulestes*, the ectoflexus of *Eodelphis* and *Didelphodon* are deep. A well-developed stylar cusp C is present on the teeth referred by Eaton (1993) to *Pariadens kirklandi* from the Cenomanian of Utah. This species has been included within the family Stagodontidae by Cifelli & Eaton (1987), but Eaton (1993) cautiously added a question mark to the familial attribution initially suggested. Fox & Naylor (1995) consider that the upper molars referred to that species by Eaton (1993) certainly do not match the stagodontid morphology since they possess a well-developed stylar cusp C. The Deltatheroida lack stylar cusp C, but a small stylar cusp D is present in *Sulestes* (Kielan-Jaworowska & Nessov 1990) and on the molars of the Gurlin Tsav skull. The absence of a conspicuous cusp in a stylar cusp C position is regarded as a plesiomorphic character state within metatherians (Fox 1975; Fox & Naylor 1986; Fox 1987; Marshall *et al.* 1990; Eaton 1993). Furthermore, Cifelli (1993a, b) and Szalay (1994) have clearly expressed that the stylar cusp C may have appeared and disappeared several times in marsupials evolution. Therefore, *Mayulestes*, which lacks a stylar cusp C, probably retains the plesiomorphic condition.
In fact, the upper molar pattern of *Mayulestes* approaches the stem marsupial morphology, according to Marshall *et al.* (1990). The following features are regarded by these authors as representing the stem marsupial upper molar morphology: (1) molars transversely wide and anteroposteriorly short; (2) ectoflexus deep, centrally located along the labial margin; (3) stylar shelf wide; (4) stylar cusps B and D prominent, with B > D; (5) stylar cusp C not developed; (6) stylar cusp A distinct, yet much smaller than D; (7) paracone and metacone very large, subequal in size, set side by side and positioned approximately midway along transverse axis of the tooth; (8) centrocrista linear; (9) conules distinct

but not enlarged; (10) protocone tall (spirelike) and not expanded, so the angle between the protocristae being acute (60°); and (11) both anterior and posterior cingula present (shelf between the anterior base of stylar cusp A and the paracone and between the posterior base of stylar cusp E and the metacone respectively). This morphology is based on that of "*Alphadon*" *creber* (specimens without stylar cusp C). *Mayulestes* shows most of the features cited by Marshall *et al.* (1990), except a posterior cingulum; *Mayulestes* also diverges from the plesiomorphic marsupial upper molar pattern in having a paracone slightly smaller than the metacone and an ectoflexus located slightly anteriorly (the two features are probably related). The condition of the Stagodontidae is similar to that of *Mayulestes* and *Allqokirus*. In his cladogram of early tribosphenic mammals, Cifelli (1993a, b) has retained the same feature (presence of a posterior cingulum) which he expressed differently: "postprotocrista of upper molars extends labially past base of metacone (double-rank postvallum/prevallid shearing)". This author regards that feature as a synapomorphy of a monophyletic group made of: (1) the Eutheria; (2) *Kokopellia*, *Zygocuspis* and *Falpetrus*; and (3) the Marsupialia [The occurrence of this character has recently been observed in *Kokopellia* (Cifelli & Muizon 1997)]. However, a postprotocrista extending labially past the metacone is absent in many metatherians: deltatheroidans, borhyaenoids, stagodontids, didelphoids, most microbiotheres, and dasyuroids. Therefore, the distribution of this feature would indicate that it appearad several times in therian evolution. However, since it is incipiently present in the Palaeocene microbiothere (*Khasia*), and absent in the Miocene (*Microbiotherium*) and Recent (*Dromiciops*) genera, it is also possible that it has been reversed (perhaps independently) in some lineages (Muizon *et al.* 1997). The molar morphology of *Mayulestes* is, hence, probably derived in the lack of a posterocingulum.

To conclude, the dentition of *Mayulestes* shows many plesiomorphic features not only for a borhyaenoid but also for a metatherian. The number of incisors of *Mayulestes* (I5/i4) is the primitive condition for marsupials and the character state "number of incisors reduced to I4/i3" is derived for the other borhyaenoids. The lack of a posterocingulum is probably a reversal within marsupials which also occurs in stagodontids, borhyaenoids, didelphoids, microbiotheres, and dasyurids. The incipiently developed features related to prevallid/postvallum shear observed in *Mayulestes* have been shown above to be of low phylogenetic value since they appeared independently in at least six groups of mammals and probably several times within some of these groups (Muizon & Lange-Badré 1997). The same is true for the increase in size from m1 to m4 and M1 to M3, a feature probably related to carnivorous diet. Consequently, the dentition of *Mayulestes* does not exhibit undoubted borhyaenoid synapomorphies since all of them are either symplesiomorphies or highly homoplastic features. The only probable derived feature of the molars of *Mayulestes* and *Allqokirus* is the great reduction of the entoconid, regarded here as a synapomorphy of the Mayulestidae. This feature certainly appears several times in borhyaenoids evolution and is therefore of low phylogenetic value. However, since the only elements of *Mayulestes* and *Allqokirus* that can be compared are M2 or 3 and m2 or 3, and since it is the only derived feature shared by the molars of the two genera, it is tentatively retained in spite of its weakness as a synapomorphy of the family. It is clear that cranial remains of *Allqokirus* are much needed to clarify this point.

The key synapomorphies of the Borhyaenoidea cannot be established on the basis of dental features but must be searched for in cranial morphology.

Bony skull

Mayulestes, a weasel-sized animal, is the smallest known borhyaenoid. Although, at first sight, the rostrum seems to be shorter than in the other borhyaenoids, the measurements in Table 1 indicate that it is even slightly longer. The rostrum of the Hathliacynidae (*Sipalocyon* and *Cladosictis*) appears to be slightly longer mainly because of the greater length of the jugal tooth row and the greater narrowness of the palate. *Mayulestes* clearly shows a shorter cheek tooth row and a wider palate between P3 and the ante-

TABLE 1. — Proportions of the length of the rostrum to the total length of the skull in borhyaenoids. **Lc**, total length of the skull form the tip of the premaxillae to the posterior extremity of the occipital condyles (in YPMPU 15046 and 15701 the occipital condyles are missing and the length of the skull is measured from the posterior border of the lambdoid crest. The error introduced is regarded here as minor); **Lr**, length of the rostrum from the anterior border of the orbit; **Lctr**, length of the cheek tooth row from anterior border of P1 to posterior border of M4, **WP3**, width of the palate between posterior roots of P3s; **WM4**, width of the palate between the M4s; **Winf**, width of the rostrum at the level of the anterior foramina of the infraorbital canal. In *Mayulestes* WM4, WP3 and Winf are approximate because of the dorsoventral crushing of the skull. All measurements are in millimeters.

	Lc	Lr	Lctr	WP3	WM4	Winf	Lr/Lc	Lctr/Lc	WP3/Lc	WM4/lr	Winf/Lc
Mayulestes (MHNC P 1249)	54	20	17	11.5e	11.5e	14.8e	0.37	0.31	0.21	0.21	0.274
Borhyaena 1 (YPM PU 15 701)	230	76	78.3	37	75	58	0.33	0.34	0.16	0.32	0.252
Borhyaena 2 (YPM PU 15 120)	195	67.2	71.3	30	63.5	42	0.33	0.35	0.14	0.36	0.251
Prothylacynus (MACN 5931)	171	52.8	–	28	48	43.5	0.31	–	0.16	0.28	0.254
Cladosictis (YPM PU 15170)	158	57.5	59	15e	32	–	0.36	0.33	0.09	0.205	0.154
Cladosictis (YPM PU 15046)	142	52	52	15.5	30	–	0.36	0.36	0.11	0.21	0.151
Sipalocyon (AMNH 9254)	112e	39e	38.5	14.5	21.5	17	0.348	0.34	0.13	0.196	0.151

rior opening of the infraorbital canal. Furthermore, in the Santa Cruz borhyaenoids, the greater concavity of the lateral side of the maxilla, in the region of the anterior foramen of the infraorbital canal, contributes to the narrowness of the rostrum and to its apparent length. In *Mayulestes*, the rostrum is not constricted at its base. Therefore, the rostrum of *Mayulestes* is relatively long (for a borhyaenoid) and robust but the palate is wider and shorter than in the Santa Cruz borhyaenoids.

The general morphology of the skull is close to that of the Borhyaenidae, from which it differs, however, by its much wider interorbital bridge. The absence of a supraorbital process is probably a plesiomorphic character since this structure is absent in several Late Cretaceous eutherians from Mongolia (*Asioryctes*, *Barunlestes*, *Kennalestes*), and in the deltatheroidan skull from Gurlin Tsav (Kielan-Jaworowska & Nessov, 1990; Szalay & Trofimov 1996). It is absent in several didelphids, in caenolestoids, in several dasyurids and in peramelids. Among the other borhyaenoids, a distinct supraorbital process is also lacking in *Borhyaena* although, in this genus, the frontal bridge is greatly widened between the orbits.

As in all the other borhyaenoids and in all generalised fossil and living marsupials, *Mayulestes* retains the plesiomorphic condition of a large orbit confluent with the temporal fossa.

The nasals of *Mayulestes* are long and posteriorly flared. They have a broad contact with the lacrimals, a plesiomorphic condition found in cynodonts, tritylodontids, *Vincelestes* (Bonaparte & Rougier 1987), *Morganucodon* (Kermack *et al.* 1981), *Sinoconodon* (Crompton & Luo 1993), *Haldanodon* (Lillegraven & Krusat 1991), *Deltatheridium* (Kielan-Jaworowska 1975a), and *Asiatherium* (Trofimov & Szalay 1994; Szalay & Trofimov 1996). Among marsupials, a nasal-lacrimal contact is present in all the borhyaenoids (except *Thylacosmilus*) and in *Wynyardia*. The derived character state is a maxilla-frontal contact which separates nasal and lacrimal. The condition of *Mayulestes* is a plesiomorphy within mammals. The nasolacrimal contact in *Wynyardia* (Gregory 1920) and the lack of contact in *Thylacosmilus* are regarded as a reversals. In the latter, this reversal is due to the hyperdevelopment of the maxillae related to the development of sabre-like canines.

The lacrimal of *Mayulestes* has a large facial wing, a plesiomorphic condition found in cynodonts, *Haldanodon* (Lillegraven & Krusat 1991), *Morganucodon* (Kermack *et al.* 1981), *Sinoconodon* (Crompton & Luo 1993), *Vincelestes* (Bonaparte & Rougier 1987), *Deltatheridium* (Kielan-Jaworowska 1975a) and *Pucadelphys* (Marshall & Muizon 1995). Furthermore, the external lacrimal foramen is doubled and opens within the orbit. This condition is plesiomorphic and it is present in cynodonts, *Morganucodon*, *Vincelestes*, *Deltatheridium* and in the other borhyaenoids. This condition is present in most didelphids, except in *Didelphis* where the

external lacrimal foramina opens dorsolaterally just anterior to the anterior extremity of the orbit. In *Thylacinus* the external lacrimal foramen is doubled and one foramen opens inside the orbit while the other opens clearly outside of the orbit anteroventrolaterally. The condition of *Mayulestes* is plesiomorphic within mammals.

Mayulestes has no palatal vacuities as is observed in the other borhyaenoids. The presence of palatal vacuities shows an important variation within mammals. They are absent in cynodonts, *Haldanodon* (Lillegraven & Krusat 1991), morganucodontids (Kermack *et al.* 1981), *Sinoconodon* (Crompton & Luo 1993), some multituberculates (*Kamptobaatar, Chulsanbaatar, Lambdopsallis, Taeniolabis*), *Vincelestes* (Bonaparte & Rougier 1987), *Deltatheridium* (Kielan-Jaworowska 1975a) and in many marsupials [*Pucadelphys, Caluromys, Sparassocynus, Dasycercus, Dasyuroides*, some species of *Sminthopsis* and *Antechinus, Myrmecobius, Dactylopsila, Petaurus* and *Dactylonax* (Marshall 1979b)]. They are generally absent in eutherians (except leporid lagomorphs, some rodents, macroscelids, erinaceids, and *Carpolestes*). Palatal vacuities are also present in some multituberculates (*Nemegtbaatar, Sloanbaatar, Bulganbaatar, Ptilodus*), in the Deltatheroida from Gurlin Tsav (Kielan-Jaworowska & Nessov 1990; Szalay & Trofimov 1996), in *Asiatherium* (Trofimov & Szalay 1994; Szalay & Trofimov 1996) and in most living and fossil marsupials (Marshall 1979b; Reig *et al.* 1987). Fox & Naylor (1995) recently observed the presence of palatal vacuities in stagodontids (*Eodelphis* and *Didelphodon*) and in *Alphadon*.

The palatal vacuities are generally regarded as plesiomorphic for marsupials (Tyndale-Biscoe 1973; Fox & Naylor 1995). However, Marshall (1979b), Archer (1982) and Marshall & Muizon (1995) stated that, since the maxillae and palatine bone in the developing skull of marsupials were generally not fenestrated [Parker (1886) noted that the fenestration occurs later in ontogeny by bone resorption], a solid palate was probably the plesiomorphic state for mammals. The high degree of variability in the presence or absence of palatal vacuities in mammals, as well as embryological observations, suggests that these structures probably appeared several times independently in and within each group, which therefore significantly reduces their phylogenetic value. *Mayulestes* and *Pucadelphys* retain the plesiomorphic condition for mammals.

The pterygoid and postpalatine region of the skull of *Mayulestes* is significantly different from that of the other borhyaenoids. The choanal fossa of *Mayulestes* is relatively wide and short anteroposteriorly. Its walls are formed essentially by the pterygoids, they are high and thin. The pterygoids have a large, hook-like hamular process which overhang (in ventral view) the basisphenoid and the alisphenoid. In the Deseadan and Santacruzian borhyaenoids (*Mayulestes* is the only pre-Deseadan borhyaenoid whose complete skull is known), the choanal fossa is long and narrow anteroposteriorly. Its walls are low, thick and formed by two bony layers, on the one hand the pterygoid medially, on the other hand the palatine anterolaterally and the alisphenoid posterolaterally. The lateral side of the wall shows a thick anteroposterior buttress. The bottom of the choanal fossa is roofed by the pterygoid. The hamular processes of the pterygoids are either lost or very reduced. As a consequence of that morphology, the plane of the palate passes smoothly to the basioccipital without the strong difference of level observed in *Mayulestes* because of the presence of very salient hamular processes. Therian pterygoids are fragile bony plates seldom preserved in fossils and unknown in Palaeogene or Cretaceous marsupials (except *Mayulestes*). In the living didelphids, the pterygoids are very fragile small bony blades (often lost during preparation) which still retain a hamular process, although much smaller than in *Mayulestes*. Well-developed pterygoid laminae and hamular processes are present in *Barunlestes* (Kielan-Jaworowska & Trofimov 1980) and *Asioryctes* (Kielan-Jaworowska 1981). The condition observed in these Late Cretaceous eutherians suggests that a pterygoid with well-developed ventral lamina and hamular process probably represents the plesiomorphic condition for therians. Therefore, *Mayulestes* retains the plesiomorphic condition; it is more plesiomorphic than the other Borhyaenoidea and the Didelphidae. As stated by Muizon (1994), the loss of the hamular process of the pterygoid is a

synapomorphy of the other borhyaenoids. However, it is noteworthy that a morphology similar to that of the other borhyaenoids is present in *Thylacinus* although, in this genus, the pterygoid plate is higher.

The jugal of *Mayulestes*, as in fossil and living marsupials, reaches the glenoid fossa posteriorly and forms a preglenoid process which receives part of the articular surface. This condition is a plesiomorphy for therians (Marshall & Muizon 1995) which is also found in *Vincelestes*, the deltatheroidan skull from Gurlin Tsav, and some eutherians. In spite of its plesiomorphic nature this feature was retained by Marshall & Kielan-Jaworowska (1992) as a synapomorphy of the Metatheria (including Deltatheroida).

The alisphenoid of *Mayulestes* has a large suture with the parietal. This character state is present in the Late Cretaceous eutherians *Asioryctes* and *Kennalestes* and in the eupantothere, *Vincelestes*. Among marsupials, it is present in fossil and living didelphids (including *Pucadelphys*), in some borhyaenoids [*Mayulestes*, *Sallacyon*, *Sipalocyon* (Archer 1976), *Notogale* (MNHN SAL 271), *Paraborhyaena* (MNHN SAL 51)], in myrmecobiids and most dasyurids (Archer 1976). It is absent in some borhyaenoids (*Borhyaena*, *Prothylacynus*), thylacinids, peramelids, vombatids, in some phascolarctids and some dasyurids (Archer 1976). *Mayulestes* therefore presents what is regarded here as the plesiomorphic state for the Theria.

The alisphenoid of *Mayulestes* makes a small contribution to the anteromedial angle of the glenoid fossa [entoglenoid process of the alisphenoid of Clemens (1966: 73)]. A much larger contribution is also present in all didelphids, in caenolestoids, in microbiotheres, in peramelids, in dasyuroids (smaller), in some perameloids and in several phascolarctoids (smaller). The alisphenoid does not participate in the glenoid fossa in the other borhyaenoids, in stagodontids, in *Hondadelphys* and in most phalangeriforms. In *Vincelestes*, the alisphenoid does not contact the glenoid fossa of the squamosal and the feature is therefore irrelevant in this genus. However, it is noteworthy that, in *Vincelestes*, a similar participation to the anteromedial angle of the glenoid fossa is achieved by the anterior lamina of the periotic. It is interesting to note here that the anterior lamina of the periotic has been regarded by Presley & Steel (1976) and Presley (1981) as homologous with the blade of the alisphenoid. A participation of the alisphenoid to the anteromedial angle of the glenoid fossa is interpreted here as a plesiomorphic character state within marsupials, which disappears independently in several lineages. *Mayulestes* retains the plesiomorphic condition within the borhyaenoids and marsupials. In Recent didelphoids, the alisphenoid is perforated by the foramen rotundum, the large foramen ovale, the entocarotid canal, and, when present, the transverse canal.

There is no transverse canal in *Mayulestes*. This structure is also absent in some borhyaenoids (*Sipalocyon*, *Borhyaena* and *Prothylacynus*). However, Marshall (1977b: 639) noted in *Lycopsis* a "tiny foramen [...] which appears to represent a rudimentary transverse canal" and a probable transverse canal is present in *Notogale* (MNHN SAL 271) from Salla-Luribay (Bolivia) and in *Cladosictis* (YPM PU 15705). There is no transverse canal in morganucodontids, multituberculates, Deltatheroida, in the Late Cretaceous eutherians from Mongolia, in some didelphids (*Caluromys*), in some dasyurids (some species of *Planigale*). A transverse canal is present in most didelphids, most dasyurids, myrmecobiids, peramelids and thylacynids. On the basis of the important variation in its size and morphology, Marshall & Muizon (1995: 71) have stated (*contra* Archer 1976) that the lack of transverse canal was likely to be a plesiomorphy for marsupials and that this structure probably appeared several times during marsupial evolution. The absence of transverse canal in *Mayulestes* would support this statement.

The term foramen ovale requires some discussion. In this work it is used to designate the foramen which transmits the mandibular branch of the trigeminal nerve without consideration of the bones surrounding it (*sensu* Kielan-Jaworowska *et al.* 1986). In *Vincelestes* (Early Cretaceous eupantothere), the foramen ovale pierces the anterior lamina of the periotic, in *Pucadelphys* and *Mayulestes* (early Palaeocene marsupials) it is limited by the alisphenoid anteriorly and by the periotic posteriorly, in

Asioryctes and *Kennalestes* (Late Cretaceous eutherians) it only pierces the alisphenoid. The designation foramen pseudovale has a variable definition according to authors (MacIntyre 1967; Archer 1976). McIntyre (1967) called foramen pseudovale in eutherians the foramen resulting in the fusion of the true foramen ovale (totally enclosed by the alisphenoid and the foramen lacerum medium). For Archer (1976, 1982), the foramen pseudovale in marsupials is the foramen called foramen ovale in this study, *i.e.* limited by the alisphenoid anteriorly and by the periotic posteriorly and through which the V3 nerve exits the skull (Archer 1976, 1982). In fact, the plesiomorph condition for marsupials is very probably that of *Pucadelphys* and *Mayulestes* (which is also present in recently discovered skulls of *Andinodelphys* from the early Palaeocene of Tiupampa). The derived condition for marsupials (found, for example, in *Didelphis*) is the formation of a short canal (the canal of the foramen ovale) in the alisphenoid which totally encloses the V3. The posterodorsal opening of the canal is the primitive true foramen ovale found in *Pucadelphys* and *Mayulestes*. It is clearly observable on a cerebral view of the basicranium of *Didelphis*. Since it represents the plesiomorph condition I suggest not to give it the name pseudovale. The anteroventral opening of the canal is a secondary formation which, in fact, would better deserve the name pseudovale than the posterodorsal opening. In order to avoid confusion with McIntyre's foramen pseudovale (fusion of foramen ovale and foramen lacerum medium), the name of secondary foramen ovale is more appropriate for the anteroventral opening of the canal of the foramen ovale (Wroe 1997).

The consequence of the formation of a canal of the foramen ovale is a superficial separation of the foramen ovale from the foramen lacerum medium. This condition is probably independent of the development of a tympanic process of the alisphenoid since *Prothylacynus* has a canal of the foramen ovale and a secondary foramen ovale although this genus did not develop a tympanic process of the alisphenoid. The lack of the tympanic process of the alisphenoid and a foramen ovale which opens between the alisphenoid and the periotic are regarded here as plesiomorphic conditions in *Mayulestes* and *Pucadelphys*. This interpretation is reinforced by the fact that Hopson & Rougier (1993: 289) stated that the didelphid condition of the embryological development of the alisphenoid and its relationships with the three branches of the trigeminal nerve represents the plesiomorphic condition for marsupials and, by extension, for all living therians.

In *Mayulestes* the foramen lacerum medium is possibly confluent with the foramen ovale, a condition observed in *Borhyaena* and the dasyurids (Marshall 1977a), which, therefore, would possess a true foramen pseudovale (*sensu* McIntyre 1967). This condition is absent in the Didelphidae and in *Pucadelphys*, and if actually present in *Mayulestes* is regarded here as apomorphic.

Mayulestes has no tympanic process of the alisphenoid. The absence of this structure in some borhyaenoids (*Borhyaena*, *Prothylacynus*, *Lycopsis*) and in *Pucadelphys* has been regarded as a derived condition (Marshall & Kielan-Jaworowska 1992). However, Muizon (1994) has suggested that the absence of alisphenoid bulla in the oldest known skulls of borhyaenoid (*Mayulestes*) and didelphoid (*Pucadelphys* and *Andinodelphys*) seems to indicate that the condition in the three genera is plesiomorphic, thus indicating that a tympanic process of the alisphenoid evolved several times independently during marsupial history. There is no tympanic process of the alisphenoid in *Borhyaena*, *Prothylacynus*, *Lycopsis*, *Sallacyon* (possibly) *Paraborhyaena* and *Thylacosmilus*. Its occurrence in the genera *Cladosictis*, *Sipalocyon* and *Notogale* (MNHN SAL 271) is regarded here as a synapomorphy of the Hathliacynidae (Muizon 1994).

Mayulestes does not have a rostral tympanic process [*sensu* Wible (1990) = tympanic wing of the petrosal part of the periotic *sensu* Archer (1976a)]. However, the small tubercle anteroventral to the fenestra cochleae is probably homologous to the rostral tympanic process. A condition similar to that of *Mayulestes* is observed in *Sipalocyon* and *Prothylacynus* (not in *Cladosictis*). Wible (1990: 199) observed in *Borhyaena* a "ridge resembling that of petrosal Type A" (a Late Cretaceous petrosal from Bug Creek Anthills, Montana). In an undescribed basicranium (MNHN SAL 271) from the late

Oligocene of Salla Luribay (Bolivia), referred to *Notogale*, a clear ridge is present on the medial side of the promontorium. In *Paraborhyaena*, the periotic bears a strong ventrally projecting process but, because of the important modifications of the auditory region of this genus (probably of the family), it is not certain that it is homologous to the rostral tympanic process of other marsupials. *Pucadelphys*, an early Palaeocene didelphoid, has a smooth promontorium while all the other members of the superfamily have a rostral tympanic process. A rostral tympanic process is present in monotremes, mutituberculates, most marsupials and in some eutherians. The homologies of that structure are not simple, since, as mentioned by Wible (1990: 199), processes on the promontorium result from several different ontogenies in Recent mammals. This author regards the lack of tympanic process as a plesiomorphy and concludes that "rostral tympanic processes of the petrosal have evolved independently a number of times within these mammalian taxa" (Wible 1990: 199). Therefore, Wible's assertions are corroborated by the morphologies of *Mayulestes* and *Pucadelphys* (which have no true rostral tympanic process) and by the observation of an undoubted rostral tympanic process in *Notogale* (MNHN SAL 271), which demonstrates that this structure appeared at least twice independently in marsupials. This is not surprising, since the presence of a rostral tympanic process is probably at least partially related to the presence of a tympanic process of the alisphenoid and/or of an alisphenoid hypotympanic sinus and, as stated above, the alisphenoid process is a structure that is likely to have evolved independently several times within marsupials.

The epitympanic recess and the alisphenoid hypotympanic sinus are structures which require special comments. The epitympanic recess is the "extension of the middle ear cavity which lies dorsal to the tympanic membrane and contains the mallear-incudal articulation" (Wible 1990: 188; see also Van der Klaauw 1931: 73; Archer 1976: 226). The posterior extremity of the epitympanic recess is the fossa incudis or fossa crus breve incudis, a deep and narrow pit where the ligament of the crus breve of the incus attaches. In all marsupials, except *Pucadelphys* and *Andinodelphys*, anterior to the epitympanic recess is a bony sinus excavated in the alisphenoid and floored by the tympanic process of the alisphenoid (absent in several borhyaenoids). It is the alisphenoid hypotympanic sinus. In the didelphoids (which are commonly regarded as bearing the basic plesiomorphic pattern for living marsupials), the epitympanic recess and the alisphenoid hypotympanic sinus are separated by the petrosal crest. The posterior slope of the crest is excavated by the epitympanic recess and the anterior slope by the posterior part of the alisphenoid hypotympanic sinus. The roof of the sinus is formed by the alisphenoid. The posterodorsal border of the roof abuts against the anterolateral border of the periotic at the base of the anterior slope of the petrosal crest. The result is that the posterior part of the roof of the sinus is formed by the periotic. The cavity of the periotic of *Didelphis virginiana*, named epitympanic recess by Wible (1990: fig. 4A) is in fact the posterior extremity of the alisphenoid hypotympanic sinus (see above). The same is probably true for the periotics illustrated in his figs 2F, 5B and D. The epitympanic recess is located posterior to the petrosal crest which is clearly observable in his figs 4A, 5A and C.

The alisphenoid hypotympanic sinus of *Mayulestes* is made of three components: the petrosal, the alisphenoid, and the squamosal (Fig. 45 and see description above). The participation of the squamosal to the sinus has been noted by Archer (1976) in three other borhyaenoids (*Sipalocyon*, *Prothylacynus* and *Borhyaena*). I have also observed it in these three genera as well as in *Cladosictis* (Muizon 1994: 210, *contra* Archer 1976: 292), in *Sallacyon*, in *Notogale* (MNHN SAL 271) and in *Paraborhyaena*. The portion of the squamosal involved partially (*Mayulestes*) or totally (other borhyaenoids) in the formation of the sinus is what has been named by Muizon (1994) the medial process of the squamosal (Fig. 45). A participation of the squamosal to the construction of the alisphenoid hypotympanic sinus is apparently absent from all the other marsupials. *Pucadelphys andinus*, a didelphoid from the early Palaeocene, also has a medial process of the squamosal but, in this species, there is no alisphenoid sinus (Fig. 46). A

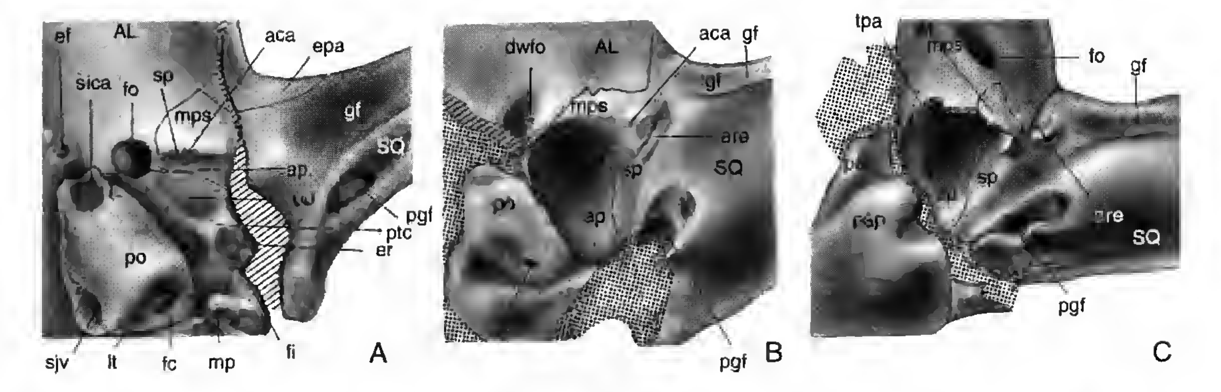


Fig. 45. — Auditory region of: **A**, *Mayulestes*; **B**, *Sallacyon*; **C**, *Cladosictis* (from Muizon 1994, modified). Abbreviations: **aca**, anterior crest of the alisphenoid hypotympanic sinus; **AL**, alisphenoid; **ap**, alisphenoid portion of the alisphenoid hypotympanic sinus; **are**, articular ridges of the squamosal for articulation of the ectotympanic; **dwfo**, dorsal wall of the foramen ovale; **ef**, entocarotid foramen; **epa**, entoglenoid process of the alisphenoid; **er**, epitympanic recess; **fc**, fenestra cochleae; **fo**, foramen ovale; **fi**, fossa incudis; **gf**, glenoid fossa; **lt**, lateral trough; **mp**, mastoid process; **mps**, medial process of the squamosal; **pap**, paroccipital process, **pgf**, postglenoid foramen; **po**, promontorium; **pp**, petrosal portion of the alisphenoid hypotympanic sinus; **ptc**, petrosal crest; **sica**, sulcus for the internal carotid artery; **sjv**, sulcus for the internal jugular vein; **sp**, squamosal portion of the alisphenoid hypotympanic sinus; **SQ**, squamosal; **tpa**, tympanic process of the alishenoid. Dotted line on figure 45C indicate the extension of the medial process of the squamosal hidden by the tympanic process of the alisphenoid. Not to scale.

similar condition is present in *Andinodelphys* (Muizon *et al.* 1997). In *Mayulestes*, a generalised borhyaenoid, the participation of the alisphenoid to the sinus is small while the periotic and the squamosal portions are much larger (Fig. 45). In younger borhyaenoids (*Sallacyon*, *Notogale*, *Sipalocyon* and *Cladosictis*), the enlargement of the sinus is mainly due to the increase in size of the alisphenoid participation. In the borhyaenoids which do not have a tympanic process of the alisphenoid, the alisphenoid sinus is opened ventrally and develops dorsally and anteriorly within the lateral wall of the skull. It may be small (*Prothylacynus*), medium-sized (*Sallacyon*, *Borhyaena*) or very large (*Paraborhyaena*). *Prothylacynus*, *Sipalocyon*, *Cladosictis* and *Paraborhyaena* have a canal of the foramen ovale and a seconday foramen ovale, totally surrounded by the alisphenoid, contrary to the condition of *Mayulestes*. In *Borhyaena*, the condition is similar ro that of *Mayulestes* since the foramen ovale is probably confluent with the foramen lacerum medium, therefore partially bordered by the periotic. In fact, it is possible to derive most of the borhyaenoid alisphenoid morphologies from a *Mayulestes* morphotype, which probably represents the plesiomorphic condition. In *Sallacyon*, the sinus is deeper than in *Mayulestes* but the organisarion of its components (alisphenoid, squamosal, and periotic) is basically similar to that in *Mayulestes*; the alisphenoid hypotympanic sinus is excavated anterodorsally in the medial process of the squamosal, posteriorly in the periotic and medially in the alisphenoid. However, because of the inadequare preservation of the only known specimen, the absence of a tympanic process of the alisphenoid and the condition of the foramen ovale are uncertain. In *Borhyaena* and *Prothylacynus*, the alisphenoid sinus develops anterodorsally and "pushes" the medial process of the squamosal within the alisphenoid, the anterior part of the sinus is still excavated in the medial process of the squamosal which is underlain by the alisphenoid; in *Borhyaena*, the foramen ovale probably has the same pattern as in *Mayulestes* [the only specimen (YPM PU 15120) available during this study is partially broken in this region of the skull]. In *Paraborhyaena*, the sinus further develops (anterodorsomedially) as a conical cavity which deeply penetrates the alisphenoid far anterior to the medial process of the squamosal; the latter is rotally internal to the sinus and forms its posterolateral wall internally; the anteroventral parr of

the sinus is excavated in the alisphenoid; the passage of the V3 is totally enclosed within the alisphenoid and there is a secondary foramen ovale. *Thylacosmilus* also has a large, anterodorsally developed alisphenoid sinus as evidenced by a rubber endocast of the middle ear cavity of FMNH P 14344 (Turnbull & Segall 1984, fig. 7). In *Sipalocyon*, *Cladosictis* and *Notogale*, the portion of the alisphenoid anterior to the medial process of the squamosal develops ventrally and posteriorly, underlies it and projects posteriorly in a well-developed tympanic process which floors the sinus; the ventral and most of the dorsal parts of the sinus are excavated in the alisphenoid; the anterolateral part of the sinus is excavated in the squamosal. The periotic portion of the sinus is small when compared to the alisphenoid and squamosal portions. There seems to be, therefore, two transformation patterns to the increase of the alisphenoid sinus in the borhyaenoids: (1) an anterodorsal expansion which excavates the alisphenoid; (2) the posteroventral development of a tympanic process of the alisphenoid. Therefore, strictly speaking, the sinus of *Mayulestes* and borhyaenoids of the first pattern, which is situated above the tympanic membrane, is an alisphenoid epitympanic sinus while that of the borhyaenoids of the second pattern, located mostly below the tympanic membrane, is physically consistent with the term alisphenoid hypotympanic sinus. Furthermore, the term alisphenoid is not very appropriate in the case of the borhyaenoids since the sinus is never excavated exclusively in this bone, in *Mayulestes* the alisphenoid portion of the sinus is even the smallest of the three. However, as mentioned above, this term is commonly used by authors (Van der Klaauw 1931; Archer 1976; Pettet & Hoffstetter 1983) and it is retained here in order to avoid confusion.

Pucadelphys andinus (early Palaeocene), the oldest didelphoid whose skull is known, does not have any auditory sinuses, a condition which has been regarded as plesiomorphic for marsupials (Marshall & Muizon 1995). An alisphenoid hypotympanic sinus is present in all the other marsupials. Contrary to statements by Marshall & Muizon (1995), the sinus is not absent in some borhyaenoids; it is only small (or reduced) in *Prothylacynus* and *Lycopsis*. *Pucadelphys* and *Mayulestes* (as expressed above) are respectively the most plesiomorphic marsupial and the most plesiomorphic borhyaenoid for this character state.

Comparison of the alisphenoid hypotympanic sinus of *Mayulestes* to that of other borhyaenoids reveals several evolutionary trends of the superfamily: (1) increase of the size of the alisphenoid hypotympanic sinus; (2) increase of the size of the alisphenoid portion of the sinus; (3) tendency to cover the sinus ventrally either by anterodorsal penetration within the alisphenoid or by posteroventral development of a tympanic process of the alisphenoid; (4) tendency to isolate the foramen ovale from the foramen lacerum medium and to enclose the course of the mandibular nerve within the alisphenoid.

As noted above, the borhyaenoids, *Pucadelphys* (Fig. 46), and *Andinodelphys* (Muizon *et al.* 1997) have a conspicuous medial process of the squamosal, a medial prolongation of the glenoid fossa of the squamosal which contacts the periotic or the alisphenoid anterior to the epitympanic recess, which reaches (almost in *Mayulestes*) the lateral border of the foramen ovale medially (this feature disappears secondarily when the alisphenoid encloses the foramen ovale), and which participates to the formation of the alisphenoid hypotympanic sinus in the former. All borhyaenoids bear such a process (*Mayulestes*, *Notogale*, *Sipalocyon*, *Cladosictis*, *Borhyaena*, *Prothylacynus*, *Lycopsis*, *Paraborhyaena*). This feature apparently absent in *Didelphodon* (UCMP 53896; Clemens 1966) and *Eodelphis* (AMNH 14169) (Matthew 1916), I have no indication on the condition in the Deltatheroida from Gurlin Tsav, and the holotype of *Asiatherium* is too crushed to allow its observation. A medial process of the squamosal is absent in the other marsupials, in *Morganucodon* (Kermack *et al.* 1981), in *Sinoconodon* (Crompton & Luo 1993), in multituberculates (Kielan-Jaworowska *et al.* 1986; Miao 1988, 1993), in *Vincelestes* (Rougier *et al.* 1992), and in *Asioryctes* from the Late Cretaceous of Mongolia (Kielan-Jaworowska 1981). Therefore, this feature is probably a synapomorphy within marsupials.

The presence of an alisphenoid hypotympanic




FIG. 46. — Auditory region of *Pucadelphys* (photo of right side of YPFB Pal 6110) to show the medial process of the squamosal. Scale bar: 2 mm.

sinus partially formed by the squamosal has been regarded as a synapomorphy of the Borhyaenoidea and the presence of a medial process of the squamosal has been regarded as a synapomorphy of *Pucadelphys* + *Andinodelphys* + Borhyaenoidea (Muizon *et al.* 1997). However, *Pucadelphys* has been referred to the Didelphidae by Marshall & Muizon (1995) on the basis of its dental morphology. If this assignment is correct, then *Pucadelphys* is the sister-group of the other didelphids in which the medial process has been lost. But one could also question the value of the dental characters used to refer *Pucadelphys* to the Didelphidae. In fact, the major features considered by Marshall & Muizon are the V-shaped centrocrista and the metacone larger than the paracone. These features have been seriously questioned by Cifelli (1990a: 315; 1990b: 328) as characters unique to didelphids since this author demonstrated that they very probably evolved independently several times among North and South American marsupials (see also Marshall *et al.* 1990, fig. 4). Furthermore, as noted above, *Pucadelphys* does not have the major tarsal synapomorphies of didelphids: the loss of the calcaneofibular (CaFi) articular facet which is clearly present in *Pucadelphys* and the presence of a proximal calcaneocuboid (CaCup) facet. It is therefore probable that *Pucadelphys andinus* is not a didelphid as stated by Marshall & Muizon (1995) but belongs to a distinct clade (sister-group of the borhyaenoids) and which independently acquired a V-shaped centrocrista (a metacone larger than the paracone is also found in borhyaenoids) and a well-developed stylar cusp C (absent in the borhyaenoids). Attribution of *Pucadelphys andinus* to a new family would explain the presence in this species of some plesiomorphic features, unique among marsupials [lack of auditory sinuses, lack of tympanic process of the alisphenoid (shared with *Mayulestes*), presence of a small anterior lamina of the petrotic] and absent in all didelphids. However, if *Pucadelphys* is actually a didelphid (or belongs to the didelphid sister-group), it is also possible that the development of an alisphenoid sinus in the didelphids was achieved with exclusion of the medial process of the squamosal which got reduced because of the increase in size of the alisphenoid in that

region of the skull. In the borhyaenoids, the development of the alisphenoid sinus has included the medial process of the squamosal. Therefore, *Pucadelphys* would represent the plesiomorphic condition for didelphoids. If this interpretation is correct then the didelphoids (including *Pucadelphys* and *Andinodelphys*) would represent the sister-group of the borhyaenoids (Muizon *et al.* 1997).

Therefore, given the fact that none of the non-dental synapomorphies of didelphids are present in *Pucadelphys* and considering the weakness of the dental synapomorphies (see above) I formally include *Pucadelphys* in a new suprageneric taxon distinct from the Didelphidae: the family **Pucadelphydae new.** *Andinodelphys* is very probably also a Pucadelphydae. However, since the study of its cranial anatomy is still in progress, the diagnose of the new family is restricted here to that of the species *Pucadelphys andinus*. The Pucadelphydae are regarded here as Didelphimorphia (*sensu* Marshall *et al.* 1990) and probable members of the superfamily Didelphoidea. However, it is noteworthy that much of the early history of marsupials is known by teeth, and it is clear that the discovery of major cranial remains of such taxa as *Alphadon*, *Peradectes* or *Pediomys* would probably radically change our poor understanding of early marsupial evolution.

Because of the presence of a medial process of the squamosal, which relates *Pucadelphys* to the borhyaenoids, the latter could possibly have their origin within unspecialised didelphoids (*i.e.* a *Pucadelphys*-like form without dental specialisations) or within their primitive sister-group (Muizon *et al.* 1997). This short discussion demonstrates again how hazardous it is to construct a phylogeny based on teeth only and how cranial and postcranial remains of early marsupials are needed to provide a safer approach to the origin and early history of the group.

The periotic of *Pucadelphys*, didelphids, caenolestoids and some dasyurids bears a small prootic canal for the transmission of the prootic canal vein which unites the lateral head vein (which passes in the posterior part of the facial sulcus) and the prootic sinus, a primary tributary of the lateral head vein (which runs in a sulcus on the lateral side of the periotic and is bordered laterally by the squamosal). The prootic sinus exits the skull through the postglenoid foramen, *via* the sphenoparietal emissary vein. The medial opening of the prootic canal is situated in a groove of the lateral side of the facial sulcus (a relict of the lateral trough of morganucodontids), posterolateral to the secondary facial foramen. The lateral opening of the prootic canal is in the ventral extremity of the sulcus for the prootic sinus, on the lateral side of the periotic. The prootic canal of marsupials passes dorsal to the petrosal crest and anterodorsal to the epitympanic recess. Among fossil marsupials, a prootic canal is present in *Pucadelphys*, in *Andinodelphys*, in petrosal of types A, B, C and D of Wible (1990). Its presence in *Didelphodon* cannot be confirmed since the corresponding part of the only known periotic of this taxon is broken (Wible 1990). The lack of a prootic canal in *Mayulestes* and in the other borhyaenoids is a synapomorphy of the superfamily. However, it is likely that this loss occurred several times during marsupial evolution (some dasyuroids, perameloids, notoryctoids and diprotodonts do not have a prootic canal), which therefore considerably reduces its phylogenetic value.

The ectotympanic of the holotype and unique specimen of *Mayulestes ferox* has been lost during fossilisation. Archer (1976a: 293) noted in *Cladosictis* a unique articulation of the ectotympanic whose "main body is intergrown laterally with the squamosal and ventrally with the tympanic wing of the alisphenoid". As he stated, this condition is unique among marsupicarnivores. I have observed it in *Cladosictis* (YPM PU 15170), *Paraborhyaena* (MNHN SAL 51) and *Notogale* (MNHN SAL 271), where the ectotympanic was preserved *in situ* (Fig. 47). I have personally removed the tympanic of YPM PU 15170 (*Cladosictis patagonicus*) which was still in contact with the squamosal. The articulation of the ectotympanic with the squamosal is characterized by several interlocking ridges and grooves. So, even if the ectotympanic is lost during fossilisation, it is still possible to know if this peculiar feature was present or not. I have observed ridges and grooves on the posteromedial angle of the glenoid fossa and on the medial side of the

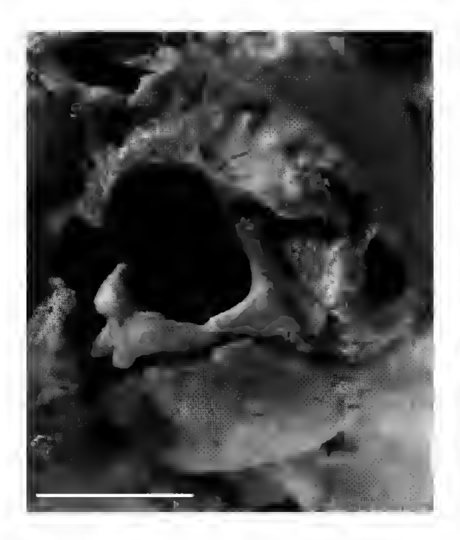
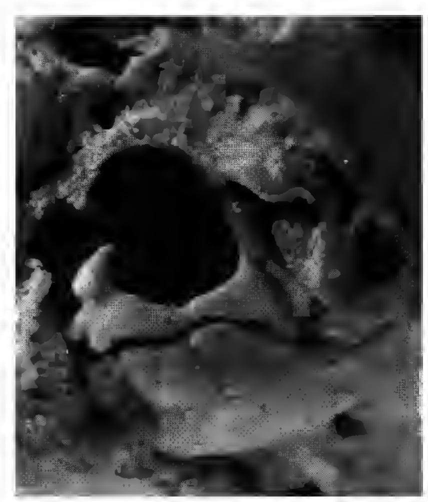



FIG. 47. — Auditory region of *Notogale* (MNHN SAL 271) to show the ectotympanic interlocked with the squamosal. Scale bar: 5 mm.

medial wall of the postglenoid foramen (the location of the ectotympanic-squamosal articulation) in *Prothylacynus* (YPM PU 15700), *Borhyaena* (YPM PU 15120), *Sipalocyon* (AMNH 9254) and *Sallacyon* (MNHN SAL 92). It is apparently absent in *Thylacosmilus*. However, considering the hyperspecialisation of the ear region of that genus, it is possible that this feature was lost in this taxon. As mentioned above, the case of *Mayulestes* is difficult since it seems to be intermediate between that of didelphids and that of the other borhyaenoids. However, the condition of *Mayulestes* is closer to that observed in didelphids and certainly not as specialised as in the other borhyaenoids. *Mayulestes* therefore retains a plesiomorphic condition within the Borhyaenoidea and it is not certain that this feature was even incipiently developed in this genus.

The periotic of *Mayulestes* has a large pars mastoidea which greatly contributes to the occiput. This is a plesiomorphic condition which also exists in several Late Cretaceous and Palaeocene marsupials (*Eodelphis*, *Didelphodon*, petrosal type A and B of Wible (1990), *Pucadelphys*). This feature is also found in didelphids, caenolestoids and most dasyuroids. All the other borhyaenoids have a reduced pars mastoidea, internal to the braincase and wedged between the squamosal and the exoccipital. *Mayulestes* retains the tribosphenid plesiomorphic condition. Among the other borhyaenoids, the occiput is formed by the occipital only in *Cladosictis*, *Sipalocyon* and *Notogale*. A large contribution of the squamosal to the occiput (in the place of the pars mastoidea) is observed in *Borhyaena*, *Prothylacynus*, *Paraborhyaena* (*contra* Muizon 1994) and *Thylacosmilus*. In this genus, the squamosal participation to the occiput is smaller than in the other three genera but this is probably related to its very special tympanic bulla (see Muizon 1994 and below).

The presence of a small true mastoid process and the absence of paroccipital process in *Mayulestes* is a plesiomorphy within mammals (Marshall & Muizon 1995). In the other borhyaenoids, since the reduced pars mastoidea is internal to the braincase, the (so-called) mastoid process does not contain any element of the pars mastoidea of the periotic but is formed by the adjunction of the paroccipital process of the exoccipital and the posttympanic process of the squamosal. It is medium-sized in *Prothylacynus* and *Paraborhyaena*. It is relatively large in *Borhyaena* where it is excavated anteriorly by a paroccipital hypotympanic sinus. It is well-developed and projects anteroventrally in *Cladosictis*, *Sipalocyon* and *Notogale*. The extreme condition is present in

Thylacosmilus where the anterior projection of the posttympanic and paroccipital processes is so hypertrophied that they contact respectively the squamosal and the alisphenoid medially to the postglenoid process and completely floor the tympanic cavity. There is no tympanic process of the alisphenoid in *Thylacosmilus*.

Conclusions on the skull

The major phylogenetic contribution of the new borhyaenoid is a better understanding of marsupial and borhyaenoid synapomorphies. Although tempting, I shall not consider here the phylogenetic relationships of the superfamily as a whole since this study will be undertaken in a work in progress which includes descriptions of the basicrania of *Sallacyon hoffstetteri* (MNHN SAL 92) and *Notogale* (MNHN SAL 271). The new data provided by these specimens allow the establishment of a phylogeny of the Borhyaenoidea represented by major cranial remains. In the following section I shall consider the problem of the diagnosis of the Borhyaenoïdea and the affinities of *Mayulestes*.

Definition of the Borhyaenoidea. The borhyaenoids have been diagnosed several times by Marshall (1976, 1977b, 1978, 1979a, 1981). However, features taken into account are often symplesiomorphies and some of them, regarded as derived, are highly homoplastic and therefore their phylogenetic value is reduced (emphasis on prevallid-postvallum shear, rapid increase in size from M1 to M3 and from m1 to m4, incipient rostral tympanic process of the periotic).

Marshall *et al.* (1990) have included in the taxon Borhyaenoidea the families Stagodontidae and Hondadelphidae. These authors have given another diagnosis of the Borhyaenoidea. In this work, the Borhyaenoidea in their traditional sense (*i.e. sensu* Muizon 1994) is the monophyletic group including the Mayulestidae + Hathliacynidae + Borhyaenidae + Proborhyaenidae + Thylacosmilidae. Marshall *et al.* (1990) have diagnosed the monophyletic clade made of Hathliacynidae + Borhyaenidae + Proborhyaenidae + Thylacosmilidae with four synapomorphies: (1) a distinct nasal-lacrimal contact; (2) the loss of subarcuate fossa of the periotic; (3) the reduction of the talonid and protocone; (4) the loss of epipubic bones. Character 1 is a symplesiomorphy. Character 2 is absent in *Mayulestes*, *Sallacyon*, *Notogale* and *Cladosictis* as these genera have a well-developed subarcuate fossa (this feature in *Mayulestes* and *Sipalocyon* has been observed by CT scanning at the Department of Geology of the University of Texas at Austin. Results of this scanning are under study by the author, R. Cifelli and T. Rowe). Character 3 is absent in *Mayulestes* and is involved in a highly homoplastic functional complex related to hypercarnivorous diet. Character 4 may be a synapomorphy of the borhyaenoids. However, it is only probable for *Mayulestes*, *Cladosictis*, *Prothylacynus* and *Lycopsis* and there is no indication that it was present in the other taxa of the superfamily. It is nevertheless tentatively retained here as a borhyaenoid synapomorphy. Therefore, the diagnosis of the Borhyaenoidea given by Marshall *et al.* (1990) is regarded here as poorly supported.

Marshall & Kielan-Jaworowska (1992: 371) have diagnosed the Borhyaenoidea with two synapomorphies: "incisors reduced to 4/3; trend for molars to increase rapidly in size from m1 to m4, M1 to M3". However, *Mayulestes* has five upper and four lower incisors and, as mentioned above, the increase in size of the molars is hardly observable in *Mayulestes* and is a specialisation related to hypercarnivorous diet found in several other groups of carnivorous mammals. It is noteworthy that the increase in size of the molars is regarded by Marshall *et al.* (1990) as a synapomorphy of the six following families (their Borhyaenoidea): Stagodontidae, Hondadelphidae, Hathliacynidae, Borhyaenidae, Proborhyaenidae and Thylacosmilidae, while Marshall & Kielan-Jaworowska (1992) regard this character as a synapomorphy of the Borhyaenoidea, a taxon which, according to these authors, does not include the Stagodontidae. Therefore, the proposed phylogeny of Marshall & Kielan-Jaworowska (1992) contradicts that of Marshall *et al.* (1990). The phylogenetic value of the character state "rapid increase in size from M1 to M3 and from m1 to m4" appears to be questionable and its weakness is corroborated by the contradiction pointed out above. Therefore, the two dental characters proposed by Marshall &

Kielan-Jaworowska (1992) are not acceptable as diagnostic of the Borhyaenoidea.

In fact, the only unique feature observed in all the skulls of borhyaenoids is the contribution of the medial process of the squamosal to the alisphenoid hypotympanic sinus. So far as known, this feature is absent from any other marsupial and is regarded here as the key-character of the Borhyaenoidea. Another suggested synapomorphy of the borhyaenoids is the loss of the prootic canal, a structure which transmits the prootic canal vein, which in turn links the sphenoparietal emissary vein to the lateral head vein in didelphids, caenolestoids and some dasyurids. However, this character state also appears in other lineages of marsupials (Wible 1990) and is consequently of lower phylogenetic value than the key-synapomorphy cited above. Furthermore, in didelphids, the fossa for the lower canine, anterior to the upper canine, is bordered by an anterolateral process of the maxilla laterally. In post-Palaeocene borhyaenoids, this process disappears and the fossa for the lower canine is opened laterally. In *Mayulestes*, the anterolateral process of the maxilla is still present but reduced, announcing therefore the condition observed in younger borhyaenoids. The reduction and loss of the anterolateral process of the maxilla is regarded here as a borhyaenoid synapomorphy. This feature is also present in *Thylacinus* but, in this genus, the fossa for the lower canine is not opened laterally (*i.e.* is completely excavated in the premaxilla), contrary to the condition observed in borhyaenoids. As mentioned above, it is probable that *Mayulestes* lacked epipubic bones. If this hypothesis is correct, the probable lack of epipubic bones in *Cladosictis*, *Prothylacynus* and *Lycopsis* (the only three other borhyaenoids known by relatively complete skeletons) would indicate that the loss of epipubic bone is another probable borhyaenoid synapomorphy.

Affinities of *Mayulestes ferox*. The above discussion of some relevant features of the skull of *Mayulestes* shows that, for most of them, it retains the plesiomorphic character state for a borhyaenoid or for marsupial. In fact, the family Mayulestidae (*Mayulestes* and *Allqokirus*) represents the sister-group of all the other members of the superfamily, which are diagnosed by six synapomorphies: (1) the pars mastoidea of the periotic, internal and not contributing to the occiput; (2) the loss of the contribution of the alisphenoid to the glenoid fossa (*i.e.* the loss of the entoglenoid process of the alisphenoid (Clemens 1966); (3) the reduction of the hamular process and laminae of the pterygoid and the formation of two crests which connect, without level difference the posterior border of the palate to the basicranium; (4) the tympanic interlocked with the squamosal; (5) the number of incisors reduced to 4/3; (6) the double-arched posterior edge of the palate. The six plesiomorphic conditions of these character states are present in *Mayulestes*. They are: (1) the pars mastoidea contributing to the occiput, (2) the presence of an entoglenoid process of the alisphenoid, (3) the hamular processes of the pterygoids well-developed and not in continuity with the basicranium, (4) the tympanic loose, attached to the squamosal by ligaments only, (5) 5/4 incisors, (6) the single-arched posterior edge of the palate. *Mayulestes* and *Allqokirus* (family Mayulestidae) are diagnosed by the reduction of the entoconid and the concomitant lingual opening of the talonid basin. It has been suggested above that, because of their lower molar morphology, the Mayulestidae could represent the sister-group of the Borhyaenidae. However, the six cranial synapomorphies of the other borhyaenoids listed above demonstrate that the hypothesis cannot be accepted so far. Nevertheless, the diagnosis of the Mayulestidae and their relationships with the other borhyaenoids have to be confirmed by the discovery of cranial remains of *Allqokirus* and *Nemolestes*. *Mayulestes* is certainly not a Hathliacynidae as stated by Marshall *et al.* (1997).

POSTCRANIAL CHARACTERS

Atlas

The intercentrum of the atlas of the holotype of *Mayulestes* is not fused to the neural arch. The type specimen of *Mayulestes ferox* is a young adult since the epiphyses of limb bones are not completely fused and the teeth are only slightly worn. A similar condition is observed in *Borhyaena tuberata* (YPM-PU 15120) where the intercentrum is not fused to the neural arch and which clearly shows incompletely ossified limb

bones. However, in *Prothylacynus patagonicus* (YPM-PU 15700) and in *Cladosictis patagonica* (YPM-PU 15702), the intercentrum of the atlas is totally fused to the dorsal arch while the limb bones are incompletely ossified. In most living didelphids the intercentrum is completely fused to the dorsal arch, contrary to what is observed in *Pucadelphys*. The condition in *Mayulestes* is plesiomorphic when compared to that of *Prothylacynus*, *Cladosictis* and resembles that of *Pucadelphys* and *Borhyaena*.

The absence of fully enclosed intervertebral foramina is a primitive condition in *Mayulestes*, *Borhyaena*, *Pucadelphys*, *Marmosa*, *Monodelphis* and *Perameles*; its presence in *Prothylacynus*, *Cladosictis* and *Sipalocyon* is a derived character state. The absence of a transverse foramen is primitive in *Mayulestes*, *Pucadelphys*, *Didelphis*, *Monodelphis*, *Metachirus* and *Asioryctes*, while its presence is a derived character state in the Santa Cruz borhyaenoids.

Axis

The axis of *Mayulestes* is clearly specialized in its large, long and triangular spinous process, a derived feature of borhyaenoids, also found in *Thylacinus*. It is more derived than in *Pucadelphys* and other didelphids, except *Didelphis*. A very long and triangular spine of the axis is also present in creodonts and carnivorans and represents an adaptation to hypercarnivorous diet since these animals kill their prey with their jaws, which requires great strength of the neck musculature. A large triangular spine of the axis is also present in *Zalambdalestes* but, in this Late Cretaceous mammal from Mongolia, the structure of the spine of the axis seems to indicate that the anterior part of the neck was immobile which would be indicative of a tendency toward saltatorial habits (Kielan-Jaworowska *et al.* 1979: 239). However, the axis of *Mayulestes* is shorter anteroposteriorly than that of the other borhyaenoids and *Thylacinus*, a condition which represents the primitive one. The lack of a totally enclosed transverse foramen is a primitive feature also found in the Palaeocene didelphoid *Pucadelphys*. In this respect, *Mayulestes* is more primitive than the other borhyaenoid, this foramen being always present in the latter.

Other cervical vertebrae

The major characteristic of the cervical vertebrae of *Mayulestes* is their relative shortness when compared to those of the other borhyaenoids. The relief of the ventral side of their centra being less pronounced than in the Santa Cruz borhyaenoids, a weaker musculature of the neck is suggested. The shorter and weaker neck is probably related to a lesser mobility of the neck. This condition is clearly less specialised than that of the other borhyaenoïds since length and strength of the neck are classical adaptations to hyperpredaceous habits also observed in carnivorans, creodonts and thylacynids. *Mayulestes* is, however, clearly more derived than several unspecialised (in this respect) didelphoids (*Pucadelphys*, *Caluromys*, *Monodelphis*, *Metachirus*, *Philander*).

Thoracic and lumbar vertebrae

As in *Pucadelphys*, the anticlinal vertebra (the vertebra where the spinal orientation reverses from a posterior orientation in the preanticlinal vertebrae to an anterior orientation in the postanticlinal vertebrae) is located much more posteriorly in *Mayulestes* than in *Cladosictis* and *Prothylacynus*, since it occurs on the lumbar vertebrae, between L3 and L5 (the spinal process of L4 is not preserved). In *Cladosictis* and *Prothylacynus*, the anticlinal vertebra is T11. The anticlinal vertebra is L1 in *Zalambdalestes*, L2 in *Pucadelphys*, between L2 and L4 (the spine of L3 is broken) in *Asiatherium*, L3 in *Metachirus* , L5 in *Marmosa* and *Caluromys*, L6 in *Monodelphis* and T11 in *Perameles* – a very dynamic curso-saltatorial Australian marsupial (Novák & Paradiso 1983). High and strongly anteriorly oriented spines of the lumbars are also observed in carnivorans (canids and felids) and creodonts, where the spine inversion commonly takes place on the last thoracics. This condition is related to a fast running. A posterior position (*i.e.* lumbar) of the inversion is observed in early marsupials and placentals and in most living genera of the conservative family Didelphidae. Therefore, *Mayulestes* would retain the primitive condition of that character state.

The size and shape of the neural spine of the lumbar vertebrae is also an important issue. The elevated and anteroposteriorly short spine of the

L5 of *Mayulestes* clearly differs from the low and anteroposteriorly long spine observed in the living didelphids. Even in *Metachirus*, a terrestrial didelphid with some cursorial and saltatorial habits (Charles-Dominique, pers. comm., 05/1996), the morphology of the spine does not fundamentally differ from that of *Caluromys*, the most arboreal living didelphid. The major difference lies in the position of the anticlinal vertebra, which is more anterior in *Metachirus* [in relation to the curso-saltatorial (terrascansorial of Szalay 1994) habits of this genus]. Canids (cursorial) and felids (leaping cursorial) generally have high and anteroposteriorly short neural spines of the lumbars. Peramelids, which are extremely agile cursorial and saltatorial marsupials have very high, short and widely separated neural spines of the lasts lumbars. This morphology is regarded here as related to cursorial and/or saltatorial locomotion more than to fossorial habits as suggested by Marshall & Sigogneau-Russell (1995). As a matter of fact, none (with one exception) of the fossorial mammals examined during this study bears this kind of neural process on the lumbar vertebrae: notoryctids, dasypodids, talpids, bathyergids, spalacids, geomyids, fossorial murids (mole-rats), meline mustelids. It is true that aardvarks have high and slender processes, however, they are not oriented anteriorly. Furthermore, it is noteworthy that, as stated by Novak & Paradiso (1983), although aardvarks are extremely efficient diggers, they can also run very fast when chased. In return, high and relatively slender (not always in some carnivorans) neural processes are found in cursorial and/or saltatorial mammals: kangaroos, canids, felids, some viverrids, murids (gerbils and hopping mice), dipodids, sciurids, chinchillids (*Lagostomus*, *Lagidium*, *Chinchilla*), caviids (*Dolichotis*). Since neither *Mayulestes* nor *Pucadelphys* show obvious cursorial adaptations, it is therefore likely that they were capable of some leaping [perhaps a sort of leaping run, as described by Jenkins (1974) in tupaiids], rather than digging as stated (for *Pucadelphys*) by Marshall & Sigogneau-Russell (1995). In *Mayulestes*, an elevated neural spine is known only on L5 (it was probably present on L4 and L6 but it is broken on L4 and L6 is not preserved). The spine of L1-3 is relatively low and long anteroposteriorly. In *Cladosictis*, the neural spines of the six lumbars are elevated, longer anteroposteriorly and more inclined anteriorly than in *Mayulestes*. In *Prothylacynus*, only the last three lumbars are known; each has a neural spine anteroposteriorly longer (more robust) than in *Mayulestes*. Because of the morphology of the spine of the last thoracics and because of the position of the anticlinal vertebra (T11), it is likely that the neural spines of the first lumbar vertebrae of *Prothylacynus* were relatively similar to those of the posterior lumbars. The morphology of the neural spine of the lumbar vertebrae (high, slender and widely separated) and the anterior position (on the last thoracics) of the anticlinal vertebra in *Cladosictis* and *Prothylacynus* indicates a more robust back musculature for these taxa, which could be interpreted as indicating some cursorial and/or probably some bounding ability. The more posterior position of the anticlinal vertebra and the morphology of the lumbar neural spine of *Mayulestes* (low in the anterior lumbars) suggests that it was less specialised in these functions than *Cladosictis* and *Prothylacynus*. It is obvious that *Mayulestes* could run relatively fast (as most living didelphids can do), but it certainly did not have what is commonly called cursorial habits. The morphology of the neural spine of the L5 would indicate some leaping or bounding ability in *Mayulestes* although to a lesser extent than in the Santa Cruz borhyaenoids because of the morphology of the neural process of the anterior lumbar and the position of the anticlinal vertebra.

The long and ventrally recurved transverse process of the last lumbars is indicative of powerful flexors of the vertebral column. Flexion of the vertebral column is performed by the quadrati lumborum and the psoas major and minor muscles when acting jointly. The size of these muscles is compatible with that of the lumbar epaxial musculature (erector spinae), which is denoted by the height of the neural processes of the posterior lumbars and the eversion of the ilia. Therefore, the morphology of the transverse processes of the last lumbars is indicative of significant mobility of the posterior part of the

TABLE 2. — Proportions of the lumbar vertebrae in some borhyaenoids and didelphids. L, length of the centrum; Wa, anterior width of the centrum. All measurements are in millimeters.

	L1			L2			L3		
	L	Wa	Wa/L	L	Wa	Wa/L	L	Wa	Wa/L
Mayulestes (MHNC 1249)	7.9	4.5	0.57	7.9	4.5	0.57	8	4.9	0.612
Cladosictis (YPM PU 15170)	20	16.4	0.82	–	–	–	–	–	–
Prothylacynus (YPM PU 15700)	–	–	–	–	–	–	–	–	–
Pucadelphys (YPFB Pal 6106)	3.7	3	0.81	4.5	2.9	0.644	4.9	2.8	0.571
Caluromys	8.3	5.2	0.626	9.4	5	0.532	10.7	5.3	0.495
Marmosa	2.9	2	0.69	3.4	1.9	0.56	3.8	1.9	0.5
Monodelphis	3.8	2.7	0.71	4.3	2.8	0.65	5.2	2.8	0.54
Metachirus	6	3.7	0.616	7	3.6	0.514	8	3.8	0.475

	L4			L5			L6		
	L	Wa	Wa/L	L	Wa	Wa/L	L	Wa	Wa/L
Mayulestes (MHNC 1249)	8.6	5	0.581	7.4	5.4	0.729	–	–	–
Cladosictis (YPM PU 15170)	–	–	–	–	–	–	22	17	0.77
Prothylacynus (YPM PU 15700)	34.5	22.5	0.652	–	–	–	–	–	–
Pucadelphys (YPFB Pal 6106)	5.5	2.8	0.509	5.5	3	0.545	4.3	3.3	0.767
Caluromys	11	5.5	0.5	11	5.3	0.48	10.5	5.4	0.514
Marmosa	3.9	2	0.512	3.5	1.9	0.54	3.1	2	0.645
Monodelphis	5.3	2.8	0.53	5.2	2.5	0.48	5.2	2.3	0.442
Metachirus	8	3.9	0.487	8	4.2	0.525	7.3	4.2	0.575

vertebral column (last thoracics and lumbars).
Jenkins (1974: 106-108) has noted four features, related to the dorsoventral mobility of the T11-T12-T13-L1 portion of the vertebral column in tree shrews. They are: (1) the ventral length of the centrum is shorter than the dorsal (neural); (2) the distance between the centres of the pre- and post articular surfaces is greater than the centrum length (measured between the centres of the nuclei pulposi); (3) the length of the zygapophyseal prearticular surface is comparable or slightly longer than that of the postarticular surface of the preceding vertebra; (4) the anterior margin of the prearticular surface is more ventral than the posterior margin which gives an anteroposterior convexity to the articular surface. In *Mayulestes*, character (1) is found on the last thoracic (T13?) but is not very well marked; it is obvious on L1-L2-L3 and was possibly present on L4. Character (2) is present on T12?, T13?, L1, L2, L3 and L5 (no measurement can be made on L4). Character (3) is present from T12? to L4 (no measurement can be made on L5). Character (4) is present in *Mayulestes* on T12?, T13?, L1 (not observable but probably present), L2, L3 and L4 (little marked). The presence of these featurse on the posterior part of the vertebral column of *Mayulestes* thus indicates great mobility. However, *Mayulestes* differs from the tree shrews since the most mobile portion seems to be located between T13? and L3 or L4 as opposed to T11 and L1 in the latter (Jenkins 1974). This difference is probably due to the fact that the anticlinal vertebra of *Mayulestes* is located much more posteriorly (L4) than in *Tupaia glis* (T10).
The centra of the last thoracic and lumbar vertebrae are proportionally longer in *Mayulestes* than in *Cladosictis* and *Prothylacynus*, while the contrary is observed on the cervicals. In this respect, *Mayulestes* resembles *Pucadelphys* and the living didelphids (*Caluromys*, *Monodelphis*, *Marmosa*, *Metachirus*). Comparison of the fourth lumbar vertebra in *Mayulestes*, Santa Cruz borhyaenoids and didelphids illustrates this differences of proportions well (Table 2). The rela-

tive size of the lumbar vertebrae of *Mayulestes*, closer to that of the didelphids than to that of the Miocene borhyaenoids, is regarded here as a plesiomorphic state within the superfamily.

Cursorial carnivorans generally have elongated, large lumbar vertebrae. The fact that Miocene borhyaenoids had relatively short centra of the lumbar vertebrae demonstrates that they were certainly not as highly specialised cursorial mammals as thylacinids, canids and some felids. However, as noted above, the Santa Cruz borhyaenoids certainly had some cursorial ability related to their hyperpredaceous habits. In *Mayulestes*, this was apparently absent or much less developed than in the Santa Cruz borhyaenoids.

Caudal vertebrae

The morphology of the caudal vertebrae of *Mayulestes* suggests some prehensile ability. A prehensile tail is observed in all living didelphids [although reduced in *Lutreolina* (Novak & Paradiso 1983)].

Marshall & Sigogneau-Russell (1995: 118, 119) have suggested that *Pucadelphys andinus* did not have a prehensile tail *contra* Muizon (1991). These authors state that "in *Didelphis*, the caudal vertebrae have specialisations associated with a prehensile tail (Krause & Jenkins 1983: 242): *e.g.* [1)] tail commonly twice or more the length of the precaudal vertebral column; [2)] a median sulcus for abductor (*sic*) muscles and tendons crosses ventrally all the vertebrae; [3)] zygapophyses are more vertical; [4)] transverse processes are broad and robust for muscle attachments and present even in most distal caudals; moreover [5)] haemal apophyses, that enclose abductor tendon and muscle, are large and developed along entire length of tail; [6)] finally, sacral spinous processes are relatively well-developed, commonly subequal to the height of the spinous processes of posterior lumbar vertebrae".

Several comments have to be made on Marshall & Sigogneau-Russell's list. First, features 2 and 3 are not cited by Krause & Jenkins (1983) as related to a prehensile tail. If feature 2 is indeed an adaptation related to a prehensile tail, why is it absent in *Marmosa*, whose tail is strongly prehensile (Novak & Paradiso 1983)? As mentioned above, the ventral sulcus, well marked in *Didelphis* and *Caluromys*, does not receive an abductor muscle but the median coccygeal aorta. On the ridges which border the sulcus laterally are inserted the sacrococcygei ventralis and medialis muscles, which form a deep furrow for the sacrococcygeal artery. The term abductor used by Marshall & Sigogneau-Russell (1995) is inappropriate for the tail since an abduction is a movement of an extremity away from the median plane; the movement they refer to is a flexion of the tail. Furthermore, the haemal arches (not apophyses) do not enclose muscles but the sacrococcygeal artery. Marshall & Sigogneau-Russell (1995: 118) state that "no such specializations except high sacral processes and very slight ventral sulcus on caudals exist in *Philander* and *Metachirus*". However, both genera also have a tail which is twice as long as the presacral vertebral column and haemal arches developed along nearly the entire length of the tail. It is true that the transverse processes of the posterior caudal are not as developed as in *Caluromys* or *Didelphis* but it is also true that they are at least as large as in the tail of *Marmosa*, one of the most prehen-sile among didelphids. Furthermore, the tail of *Philander* is reported as prehensile (Novak & Paradiso 1983 and Julien-La Ferrière pers. comm.). Novak & Paradiso (1983: 12) state that the didelphid tail is "long, scaly, very scantily haired and prehensile". Concerning *Lutreolina*, one of the most terrestrial genus, these authors state that the tail is not as prehensile as in other didelphids. They also report the observation of an individual of *Monodelphis domestica* carrying a piece of paper by curling its tail downward around the paper. Therefore, all didelphids appear to have some degree of prehensility of the tail. The greater ability is found in *Didelphis*, *Marmosa*, *Caluromys* and *Philander* and the lesser ability is found in *Monodelphis*, *Lutreolina* and *Lestodelphys*.

Marshall & Sigogneau-Russell (1995: 119) have stated that there was no indication that the tail of *Pucadelphys* was prehensile. However, the posterior caudal vertebrae of *Pucadelphys* bear large and robust transverse processes and the tail is long (estimation of 30 vertebrae). The C6 and C7 of *Pucadelphys* are strikingly similar to C5

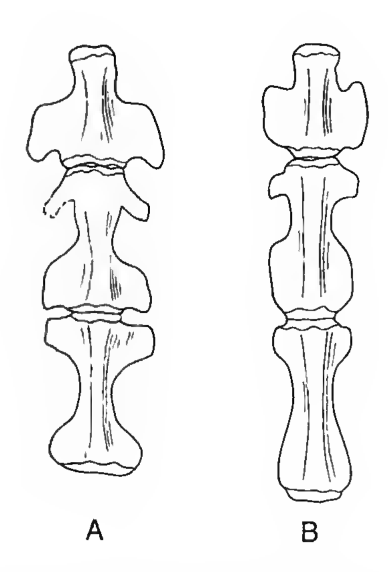


FIG. 48. — Anterior caudal vertebrae of: **A**, *Pucadelphys* (C6-C8); **B**, *Caluromys* (C5-C7). Not to scale.

and C6 of *Caluromys*, the most arboreal living didelphid (Fig. 48). In the C6 of *Pucadelphys* and C5 of *Caluromys*, the transverse process is located posteriorly on the centrum and occupies more than half of its length. It is much longer than in the preceding vertebra. The C6 of *Caluromys* and the C7 of *Pucadelphys* differ from the respective preceding vertebra by the adjunction of a small anterior transverse process, much shorter anteroposteriorly than the long posterior transverse process. In the posterior caudal vertebrae of the two genera, the transverse processes are well-developed, as large as in *Didelphis* and certainly much larger than in *Marmosa* or *Philander*. Because of the large transverse processes of C6 to C9 (YPFB Pal 6106) and in C16? and C17? (YPFB Pal 6110), I consider that *Pucadelphys* had a prehensile tail. It is not possible to evaluate the degree of prehensility of the tail since the tail of *Pucadelphys* is not complete in the available specimens and because there seems to be some inconstancy in the correlation between the anatomical features regarded as related to a prehensile tail and the actual prehensility of the tail in living didelphids. The statement by Marshall & Sigogneau-Russell (1995) that there were no haemal arches in *Pucadelphys* is contradicted by the presence of a fragment of arch still present between C7 and C8 of YPFB Pal 6106 and of a partial arch below C4 of YPFB Pal 6110. The lack of most haemal arches in *Pucadelphys* is regarded here as a loss due to fossilisation. The only feature mentioned by Krause & Jenkins (1983) and which is absent in *Pucadelphys* is the large size of the spinous processes of the sacral vertebrae. In *Pucadelphys*, these processes are broken, but in view of their smaller diameter it is likely that they were not as high as those of the last lumbar. However, it is noteworthy that the most important movements of a prehensile tail are the flexions of the tail and the spinous process of the sacral vertebrae bears attachment for extensor muscles of the tail.

The two posterior caudal vertebrae of *Mayulestes* are extremely similar to the C9 of *Pucadelphys* and to the C7 and C8 of *Caluromys*, mainly in the large size of their anterior and posterior transverse processes (Fig. 49). They are, however, longer than in *Pucadelphys* and slightly shorter than in *Caluromys*. Because of this morphological similarity it is probable that *Mayulestes* had a prehensile tail.

Cartmill (1974: 51) has stated that most prehensile-tail animals (except primates) "practically never make leaps of any distance and generally move cautiously from one support to another". As shown below, it is probable that *Mayulestes* was a relatively agile animal capable of some leaping run, as tree shrews, although certainly slower. Therefore, a contradiction would exist between the prehensility of the tail of *Mayulestes* and the suggested agility of the animal. First, it is necessary to keep in mind that only four caudal vertebrae of *Mayulestes* are known, therefore, the anatomical support of the prehensile tail of *Mayulestes* is still relatively weak. Furthermore, if the tail of *Mayulestes* was indeed prehensile, it is possible that this function was little used by the animal and being lost in favour of an increasing agility of the locomotion. The tail could have kept the characters and the ability of prehensility although it was not (or little) used as such. A living example of this condition is the terrestrial didelphid *Metachirus* which indeed has a prehensile tail but which does not use it for climbing. The same can be said of the aquatic didelphid *Chironectes*. Another interpretation (see below

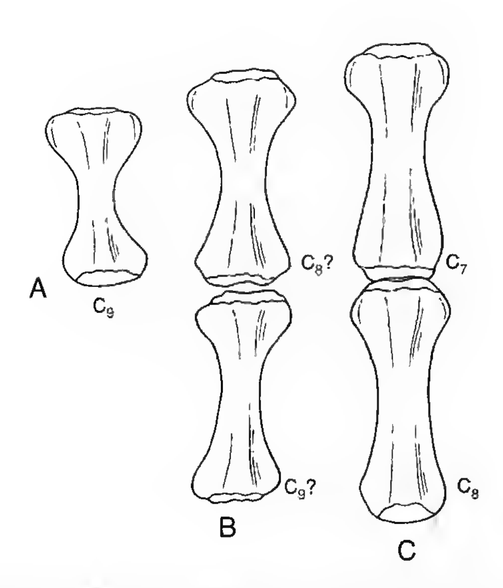


FIG. 49. — Posterior caudal vertebrae of: **A**, *Pucadelphys* (C_9); **B**, *Mayulestes* (C_8? and C_9?); **C**, *Caluromys* (C_7 and C_8). Not to scale.

for discussion) would be to consider that the agility of the animal was mainly used on the ground (like *Metachirus*) and that the arboreal locomotion was slower. In other respect, it is noteworthy that the great jumping agility of the didelphid genus *Marmosa* contradicts Cartmill's assesement.

The inferred presence of a prehensile tail in *Pucadelphys* (probably) and *Mayulestes* (possibly) suggests that these animals are likely to have had some arboreal habits. Furthermore, the generalised occurrence of a prehensile tail in didelphids (to various extent according to the taxa), the most primitive family of living marsupials, would favour the idea that a prehensile tail is a plesiomorphic character state for marsupials and seems to reinforce the hypothesis (Szalay 1984, 1994) that early marsupials were primarily arboreal (see below for discussion).

Forelimb

Scapula. The anatomy of the scapula of *Mayulestes* denotes a more robust constitution of the shoulder musculature than in other borhyaenoids and most didelphids, but is similar to that of *Caluromys*. The coracoid process is large, strongly recurved and projects more proximally than the glenoid fossa; the acromion projects proximally below the glenoid fossa and anteriorly beyond the supraglenoid process. The latter receives the origin of the coracobrachialis muscle whose insertion is located on the posteromedial border of the proximal half of the diaphysis of the humerus The coracobrachialis is an adductor of the forelimb and a flexor of the shoulder. On the acromion (on the hamatus and suprahamatus processes) and on the ventral two thirds of the scapular spine attaches part of the origin of the deltoideus (acromial and spinal) muscle. The insertion of the deltoideus muscle is on the distal two thirds of the deltopectoral crest on the humerus. On the ventral third of the spine and on the anterior margin of the acromion attaches the insertion of the atlantoacromialis muscle (Jenkins & Weijs 1979), probably a part of the omotransversarius. The origin of the atlantoacromialis muscle is on the posterior side of the wing of the atlas. The deltoid muscle is an abductor of the shoulder and a flexor of the arm when combined with the action of the teres major muscle. The atlantoacromialis pulls the scapula anteriorly and makes it rotate anticlockwise. The morphology of the coracoid process and acromion of the scapula of *Mayulestes*, projected proximally and anteroproximally respectively, denotes the great strength of those muscles and, therefore, the strength of the shoulder articulation. In arboreal mammals, the acromion and the coracoid process are generally well-developed and ventrally (and anteriorly for the former) projected, often to a much greater extent than in *Mayulestes* (tree shrews, possums, opossums, primates, tree sloths, *Cyclopes*, kinkajou, coendou; Fig. 50). This morphology has been related to arboreal habits (Corruccini & Ciochon 1976; Ciochon & Corruccini 1977). The proximal elongation of the acromion is likely to be related to improvement of the leverage for the deltoideus (Inman *et al.* 1944; Larson 1993), an abductor of the arm. Furthermore, a dorsoposterior elongation of the posterodorsal angle of the scapula, as it is observed in *Mayulestes* and *Caluromys*, is also present in most arboreal mammals (Fig. 50). This is especially obvious in primates (Roberts 1974; Larson 1993). The anterior projection of the acromion and the posterodorsal elongation of the posterior angle of

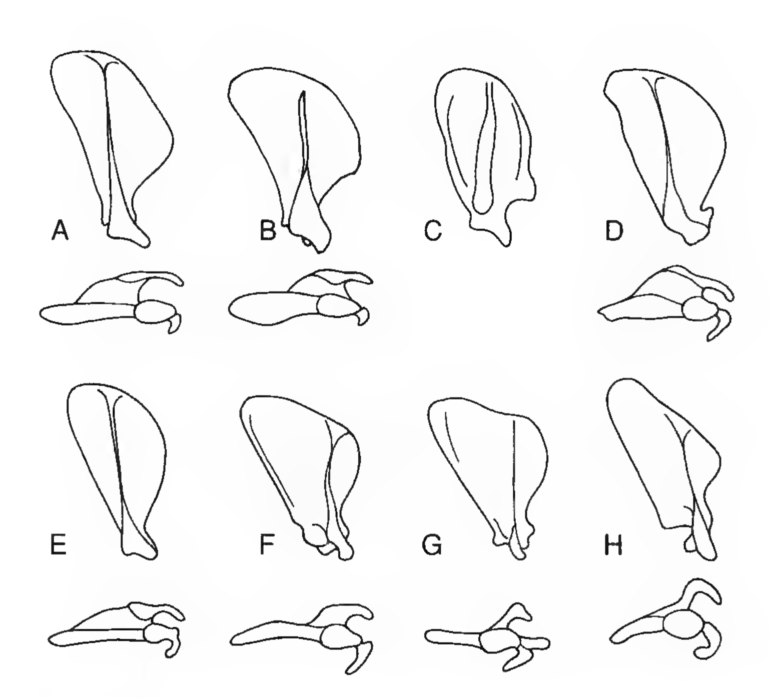


FIG. 50. — Right scapulae in lateral (top) and proximal (bottom) views: **A**, *Mayulestes*; **B**, *Caluromys*; **C**, *Cladosictis*, **D**, *Sciurus*; **E**, *Tupaia*; **F**, *Propithecus*; **G**, *Colobus*; **H**, *Hylobates*. Not to scale.

the scapula can be related to great ability of anterior extension of the forelimb since, during this movement, at the end of the extension, a better protraction of the limb is produced by an anticlockwise rotation of the scapula. Such movements are performed in acrobatic arboreal activities. As demonstrated by Larson (1993) in arboreal primates, a raised-arm position provokes an important rotation of the scapula while, in terrestrial primates, the movements of the scapula are mainly anteroposterior translations and the rotation is weak. In arboreal primates, scapular rotation is brought about by the action of a muscular couple (Inman *et al.* 1944; Larson 1993). The upper unit is the cranial trapezius and the lower unit is the caudal trapezius and the caudal serratus anterior muscles (Fig. 51). In *Didelphis*, the couple of muscles acting during the anterior extension of the forelimb (anticlockwise rotation of the scapula) has an upper unit made of the serratus ventralis thoracis and the caudal portion of the trapezius and a lower unit made of the atlantoacromialis and the anterior portion of the trapezius. In *Didelphis*, the serratus ventralis thoracis takes origin from the first eight or nine ribs and inserts on the caudal angle of the scapula; the trapezius originates from the nucchal crest and the supraspinous ligament from the occiput to the level of the thirteenth thoracic vertebra. Its anterior portion inserts on the anterior edge of the spine of the scapula, while its posterior portion inserts on the posterior edge of the distal third of the spine. The atlantoactomialis links the posterior side of the wing of the atlas to the acromion and the proximal third of the spine (Jenkins & Weijs 1979). Acting jointly, these three muscles rotate the scapula counterclockwise and exert an anteriorly directed force on the acromion and proximal third of the scapular spine and a posteriorly directed force on the posterodorsal angle of the scapula.

The two features of the scapula discussed above (anterior position of the acromion and posterodorsal elongation of the posterodorsal angle) are not as developed on the scapula of *Mayulestes* as on the scapulae of highly arboreal primates, but they approach the condition observed in *Caluromys*, the most arboreal didelphid (Fig. 50). The proportions and relative sizes of the supra- and infraspinatus fossae are difficult to explain

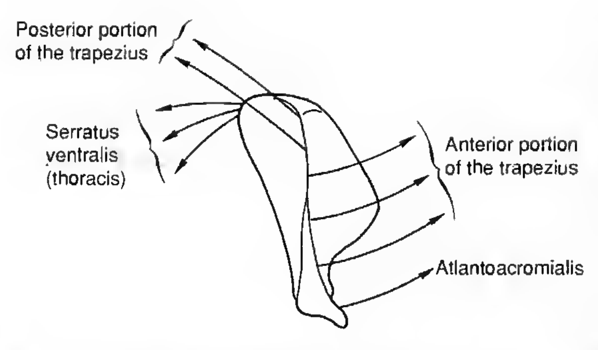


FIG. 51. — Scapulothoracic muscular couple involved in the rotation of the scapula in *Mayulestes* [based upon Larson (1993, fig. 2.5) and Jenkins & Weijs (1979)]. The anteroventral unit is made of the atlantoacromialis and the anterior portion of the trapezius; the posterodorsal unit is made of the serratus ventralis thoracis and the posterior portion of the trapezius.

mechanically in *Mayulestes*. In arboreal primates, the infraspinatus fossa and muscle are generally larger than the supraspinatus (Roberts 1974) while the contrary is observed in *Mayulestes*. However, squirrels have a morphology of the scapula very similar to that of *Mayulestes*. The posterodorsal angle is strongly elongated, the acromion is ventrally and anteriorly projected, the coracoid process is very long and developed ventrally (much longer than in *Mayulestes* and any didelphids), the supraspinatus fossa is large, triangular and the infraspinatus fossa is deep long, straight and narrow and its posterior edge is almost parallel to the plane of the spine. Squirrels are well-known to be non-suspensorial arboreal rodents while many arboreal primates are at least partially suspensorial. The similarities between the scapulae of *Mayulestes* and sciurids are possibly related to similar positional behaviours. Therefore, many aspects of the morphology of the scapula of *Mayulestes* are similar to those observed in highly arboreal mammals. It is mechanically consistent, with a strong commitment to arboreality, probably to a higher degree than in most living didelphids (except *Caluromys*).

In *Pucadelphys*, the morphology of the scapula is not completely known. However, the best preserved scapula of *Pucadelphys andinus* (Fig. 18) shows important similarities with that of *Mayulestes*: ventral and anterior development of the acromion and the deep and narrow infraspinatus fossa. According to the above discussion these features are apparently consistent with well-developed arboreal habits.

Humerus, ulna and radius. The proximal extremity of the humerus of *Mayulestes* resembles that of the didelphids more than that of the other borhyaenoids. The head is relatively circular (in proximal view), oriented more proximally than posteriorly and slightly higher than the greater tubercle (Table 3). In *Prothylacynus*, the head has a more posterior orientation and is lower than the greater tubercle, two features well-developed in cursorial mammals (for instance *Thylacinus*). Arboreal mammals tend to have a head of the humerus proximally oriented and a low greater tubercle in order to increase the mobility of the joint. In cursorial mammals, a great multidirectional mobility of the articulation is not essential since the movement of the forelimb is mostly anteroposterior and importance is given to the power of the movement. Therefore, modifications of the joint are focused toward stabilisation of the scapulohumeral joint; according to Larson & Stern (1989), that is the most significant role of the supraspinatus (which is inserted on the greater tubercle) in terrestrial primates. The infraspinatus is also involved in that function since it is inserted on the greater tubercle slightly more proximally than the supraspinatus.

TABLE 3. — Proportion of the head of the humerus in various marsupials. L, Length; W, width. All measurements are in millimeters.

	L	W	W/L
Mayulestes (MHNC 1249)	5.2	5.6	1.07
Prothylacynus (YPM PU15700)	2.9	2.9	1
Cladosictis (YPM PU 15831)	1.77	1.35	0.76
Cladosictis (YPM PU 15556)	1.65e	1.3	0.78
Pucadelphys (YPFB Pal 6106)	3.2	3.2	1
Caluromys	6	5.8	0.96
Didelphis	10.3	9.6	0.93
Marmosa	2.3	2.1	0.91
Monodelphis	3.6	3.4	0.94
Metachirus	7.6	5.9	0.77
Thylacinus	27	21.5	0.79
Tupaia	19	16	0.84
Sciurus	7.2	6.8	0.94
Vulpes	3.2	3	0.93

TABLE 4. — Relative height of the spine of the scapula in various arboreal and terrestrial mammals. **H**, greatest height of the spine approximately in its middle part; **L**, length of the spine at its base from its distal notch (*i.e.* at base of the acromion) to the proximal extremity. All measurements are in millimeters.

	H	L	L/H
Mayulestes (MHNC 1249)	4.8	19.6	0.244
Pucadelphys (YPFB Pal 6105)	2.9e	14.4	0.2
Didelphis	6	33.2	0.18
Caluromys 1	4.2	17.6	0.23
Caluromys 2	4.3	18.5	0.23
Marmosa	2.1	9.5	0.22
Monodelphis	3.2	14.3	0.22
Metachirus 1	4.6	25.3	0.18
Metachirus 2	3.5	20	0.175
Philander	6	30	0.2
Sciurus	7	27	0.26
Tupaia	3.3	14.4	0.23
Potos	9.4	47.8	0.196
Herpestes	5.5	31.2	0.176
Mustela	4.3	35	0.12

The authors also conclude that this muscle (supraspinatus) and, therefore, the size of the greater tubercle are not related to speed or power of the movement (Larson & Stern 1989 1992). A small greater tubercle and a humeral head proximally oriented generate a greater mobility of the shoulder, which is required in arboreal life. However, as mentioned by Larson & Stern (1989), the scapulohumeral joint also needs stabilisation during acrobatic behaviour. The authors concluded that "the only way for an animal with a lower greater tubercle to deal with these heavy demands on the supraspinatus for brachial elevation and joint stabilisation is to increase the overall size of the supraspinatus itself" (Larson 1993: 60). There are two ways of increasing the size of the supraspinatus muscle, either by increasing the size of the fossa or by increasing the elevation of the spine. The spine of *Mayulestes* is more elevated than that of *Caluromys* but lower than in sciurids and approaches that of tupaiids. It is relatively much more robust than in *Metachirus*, a terrestrial didelphid. Table 4 compares the relative height of the scapular spine in several marsupials, one sciurid, one tupaid, one arboreal carnivore and two terrestrial non-cursorial carnivores.

The deltoid crest of *Mayulestes* is shorter than in the Santa Cruz borhyaenoids but matches the length observed in the living didelphids (Table 5).

The very salient tricipital crest of *Mayulestes* received the origin of a robust caput laterale of the triceps brachii muscle. The insertion of this head of the triceps is on the olecranon of the ulna with the capitis mediale and longum. The strength of the triceps brachii of *Mayulestes* is also revealed by the great length and size of the olecranon of the ulna and by the important anterior curvature of the proximal third of the shaft of that bone. This morphology indicates important tractions of the triceps on the olecranon. A similar morphology of the olecranon is found in living didelphids, being strongly emphasised in the most arboreal taxa (*Caluromys*, *Marmosa*). It is also obvious in *Pucadelphys* (Figs 25, 52). In *Caluromys* and *Mayulestes*, the tension of the triceps brachii on the olecranon is even greater since its anteroproximal angle is strongly elongated anteroproximally. Such a morphology of the proximal half of the ulna exists, to various extents, in many arboreal [especially arboreal quadrupedal or arboscansorial (Szalay 1994)] mammals: didelphids, phalangerids, *Nasua*, *Potos*, sciurids and tupaiids. In primates and xenarthrans there is a tendency to reduce the length of the olecranon in order to allow a greater extension of the elbow. The posterior edge of the ulna is straight in terrestrial mammals, even concave in highly cursorial taxa, with the olecranon posteriorly oriented (Bown *et al.* 1982). In the Santa Cruz borhyaenoids the proximal third of the ulna is not bent anteriorly. In *Prothylacynus* and *Cladosictis*, the posterior border of the ulna is concavoconvex but the bone is globally straight. In *Borhyaena*, the posterior border of the ulna is straight in its proximal half and concave in its distal half and the olecranon is long, robust and has a very quadrate proximal extremity. The morphology of the ulna of *Borhyaena* is indicative of a terrestrial mammal with some cursorial ability. The ulna of *Thylacinus* (a cursorial marsupial) is similar to that of *Borhyaena*, but more gracile and more recurved posteriorly.

The distal extremity of the humerus of

TABLE 5. — Relative length of the deltoid crest. **Lh**, total length of the humerus; **Lcr**, length of the deltoid crest. All measurements are in millimeters.

	Lh	Lcr	Lcr/Lh
Mayulestes left (MHNC 1249)	32.3	18.4	0.57
Mayulestes right (MHNC 1249)	34.6	19.2	0.555
Prothylacynus (YPM PU 15700)	161	103	0.639
Cladosictis (YPM PU 15702)	113	80	0.708
Pucadelphys (YPFB Pal 6106)	17.8	9.5	0.53
Didelphis	62.7	35	0.558
Caluromys	40.8	21.7	0.53
Marmosa	14.4	7.8	0.54
Philander	42.8	22.8	0.53
Monodelphis	20.5	12	0.585
Metachirus	31.7	16.4	0.51
Thylacinus	178	129	0.724

Mayulestes bears a very strong lateral epicondyloid crest and a robust distomedially elongated medial epicondyle. On the posterior side of the epicondyloid crest attaches the distal part of the origin of the caput mediale of the triceps brachii, a powerful extensor of the elbow whose insertion is on the anterior, anteromedial and anterolateral surface of the olecranon of the ulna (the distal portion of the caput medial of the triceps is the anconeus muscle, which is apparently fused to the medial head of the triceps in dasyurids (Kielan-Jaworowska & Gambaryan 1994)]. On the anterior side of the lateral epicondyloid crest and on the lateral epicondyle attach the origins of the extensor muscles of carpus and digits and the brachioradialis muscle. On the medial epicondyle are the origins of the flexors muscles of carpus and digits, the epitrochleoanconeus and the pronator teres. Therefore, the morphology of the distal extremity of the humerus of *Mayulestes* indicates the power of the flexion and extension of the manus and a good ability in the pronation-supination movements. The great depth of the fossa on the medial side of the proximal third of the ulna for the origins of the flexor carpi ulnaris and flexor digitorum profundus muscles as well as the strong medial bending of the proximal third of the bone also contribute to suggest ability of powerful flexion of the digits and manus, for instance for grasping branches. These aspects of the morphology of the elbow of *Mayulestes* resemble those of *Caluromys* (the most arboreal living didelphid) and *Pucadelphys* (although the features mentioned above are less pronounced in this genus; Fig. 52). They are more pronounced in *Mayulestes* than in most

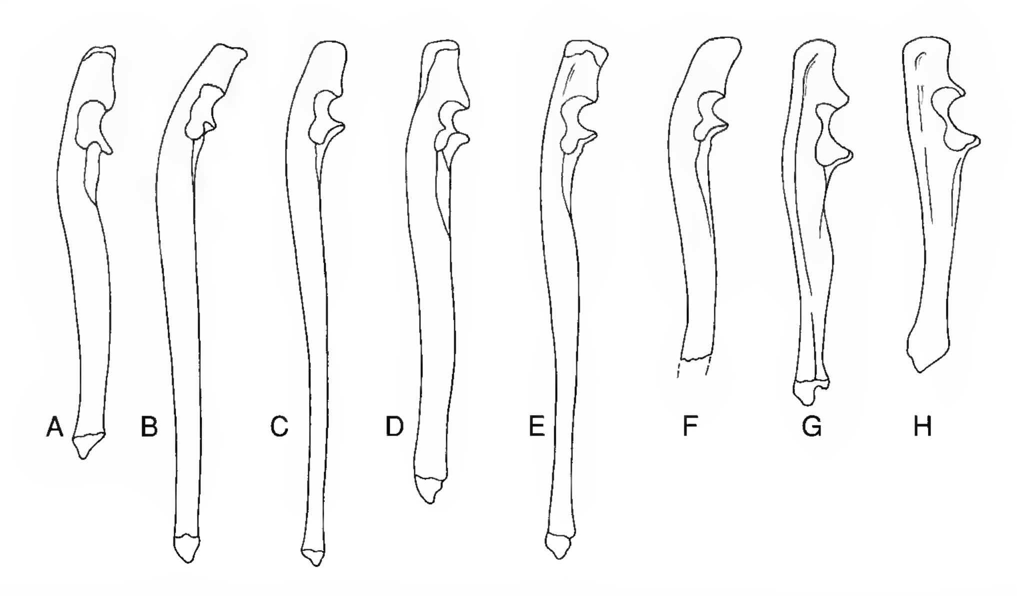


FIG. 52. — Lateral view of the left ulna in several marsupials: **A**, *Mayulestes*; **B**, *Caluromys*; **C**, *Marmosa*; **D**, *Didelphis*; **E**, *Metachirus*; **F**, *Pucadelphys*; **G**, *Prothylacynus*; **H**, *Borhyaena*. Not to scale.

other living didelphids and Santa Cruz borhyaenoids. *Potos* and *Nasua*, arboreal and semiarboreal carnivorans respectively, have the same modification of the elbow responsible for powerful flexion and extension of the manus and digits. Sciurids also have a well-developed lateral epicondyloid crest, a distomedially projecting medial epicondyle and a medially bent proximal extremity of the ulna. A long and anteriorly bent olecranon has been regarded as related to arboreal quadrupedalisme since, in such forms, the forelimb is always in partial flexion and the extensors of the elbow are always resisting to flexion (Bown *et al.* 1982). This feature, extremely developed in a predator like *Mayulestes*, could also indicate bounding or leaping ability.

On the ulna of *Mayulestes*, the trochlear notch is more open (in medial view) and shallower than in the Santa Cruz Borhyaenoids and some didelphids (*Didelphis*, *Metachirus*). Furthermore, the trochlear and radial notches form an angle of approximately 120° in anterior view. As mentioned above, this condition is found in the most arboreal didelphids (*Caluromys*, *Marmosa*, *Didelphis*). In a cursorial marsupial such as the thylacine and in the sub-cursorial *Borhyaena* (see below), the trochlear notch is less open than in *Mayulestes* and the angle between the trochlear and radial notches (in anterior view) is clearly inferior to 90°. In other words, the trochlear and radial notches are well-separated by an elevated crest and the radial notch is well-excavated in terrestrial (*a priori* in cursorial) forms, while the contrary is true in arboreal quadrupeds. The arboreal morphology (*Caluromys*, *Didelphis* and *Mayulestes*) would indicate an elbow that does not receive much articular stress and does not require an important stability of the joint and, therefore, would designate relatively slow animals. However, this morphology of the radioulnar articulation also indicates a great mobility related to pronation-supination movements. This is corroborated by the great development of the supinator crest, fossa and pronator ridge. In the very agile squirrels, the trochlear notch is similar to that of *Didelphis*, the angulation between both articular surfaces approaches 120° and the radial notch is very shallow. Furthermore, in *Mayulestes*, the long and robust olecranon indicates a powerful triceps and the strong attachment crest of the ulnar collateral ligament medially are indications of a fairly stable elbow joint, which is in agreement with the postulated activity. Therefore, the morphology of the proximal articulation of the ulna of *Mayulestes* seems to be compatible with agility. Whatever that may be, it is clear that the morphology of the humeral articulation of the ulna of *Mayulestes* resembles that of *Caluromys*, more than that of any other didelphid or borhyaenoid. The apparent weakness of the elbow joint noted on the articular surfaces was probably compensated for by ligaments and muscles as in active tupaiids and sciurids. It is also noteworthy that the relative breadth of the trochlear notch, when compared to that of *Caluromys*, is a factor of stability of the elbow, as indicated by Fleagle *et al.* (1975: 136) for the ulna of *Aegyptopithecus*.

Bown *et al.* (1982: 626) have listed several features of the ulna which are related to arboreal quadrupedalism. They are: (1) long olecranon extended proximally in line with the shaft; (2) trochlear notch relatively shallow with a low coronoid process; (3) small radial notch not deeply excavated; (4) anteroposteriorly deep ulnar shaft, posteriorly convex. According to these criteria, the ulna of *Mayulestes* is that of a highly arboreal quadruped.

On the radius, the proximal articulation with the capitulum of the humerus is transversally elongated and, as preserved, does not suggest pronounced pronation-supination movements, which contradicts the above statements. The condition of *Mayulestes* is similar to that of *Borhyaena* and *Cladosictis*, but differs from *Prothylacynus* where the radiohumeral articulation is more oval-shaped and less transverse. Although, as noted above, the morphology of *Mayulestes* is probably the result of some post-mortem erosion and/or deformation, it is likely that its pronation-supination ability was slightly less developed than that of living didelphids. It is probable that the movements had less amplitude, although it is difficult to determine to which extent. In this respect, it is noteworthy that, in living didelphids which have well-developed pronation-supination, the proximal articulation of the radius is never totally circular as in arboreal pri-

mates or tree sloths but is oval, although less transverse than in *Mayulestes*, *Cladosictis* and *Borhyaena*. The relatively oval-shaped proximal articulation of the radius of *Prothylacynus* indicates superior pronation-supination ability when compared to the other Santa Cruz borhyaenoids.

Metacarpus. As noted above, both extremities of McV are flattened in the same plane. Therefore, since the articulation with McIV (on the palmar side of the proximal epiphysis of McV) is roughly perpendicular to the dorsopalmar plane of the hand, the articulation between the McV and the first phalanx of the digit is also perpendicular to the dorsopalmar plane of the manus. This indicates that digit V had a plane of flexion which tended to be at 90° with that of the other fingers. This condition (which is approaching that of McI and McII in man) would indicate an important ability of prehensility of the manus, which obviously facilitates grasping and is clearly useful for climbing trees.

Furthermore, the medially recurved distal extremity of the McV (also observed, but to a lesser extent, in the living didelphids) tends to shift the phalanges of the finger toward the centre of the manus. This condition is also useful for grasping, an action fundamental in didelphid arboreality.

Hindlimb

Innominate. The ilium of *Mayulestes* is proportionally slightly longer than in *Cladosictis* and *Prothylacynus* but as shown in table 6 the difference is more important regarding living didelphids, whose ilia are clearly long and narrow. Such a morphology is found in a large number of living marsupials (it is absent in *Thylacinus* and *Perameles*). The Palaeocene didelphoid *Pucadelphys andinus* has an ilium relatively shorter than that of the living didelphids and resembles *Mayulestes* in this point. Therefore, the oldest known borhyaenoid has an ilium longer than the younger forms and the oldest known didelphoid has an ilium shorter than the Recent didelphids. What then is the primitive morphology of the ilium? Short or long? Marshall & Sigogneau-Russell (1995) regarded the dorsoventral expansion of the wing of the ilium in *Pucadelphys* as a specialisation but consider its shortness as a primitive state. Triconodonts have a narrow and elongate ilium (Jenkins & Parrington 1976) although, apparently, not as long as in the living didelphids. The ilium of *Henkelotherium* is longer than that of *Mayulestes* (Krebs 1991). The same is true in Asiatic (Kielan-Jaworowska & Gambaryan 1994) and North American multituberculates (Krause &

TABLE 6. — Relative length of the ilium in various marsupials and placentals. **Hil**, maximum height of the ilium at mid-length; **Lil**, length of the ilium; **Lt**, total length of the innominate. All measurements are in millimeters.

	Lil	Lt	Lil/Lt	Hil	Hil/Lil
Mayulestes (MHNC 1249)	25.2	44	0.572	6.5	0.258
Cladosictis (YPM PU 15702)	70.5	124	0.568	26	0.368
Cladosictis (YPM PU 15170)	60e	106	0.566	21	0.35
Prothylacynus (YPM PU 15700)	97	182e	0.538	35.5	0.364
Thylacinus	104	182.4	0.57		
Pucadelphys (YPFB Pal 6106)	15	26.4	0.568	5	0.33
Didelphis	50.5	75.5	0.668	12	0.23
Metachirus	26.2	40	0.65	6.4	0.24
Caluromys	30.3	45	0.677	6.2	0.2
Marmosa	11.8	17	0.69	1.6	0.13
Phalanger	47.5	75.5	0.63	10.5	0.22
Perameles	49.5	85.7	0.56	17.8	0.36
Sciurus	24.3	41	0.59		
Nasua	56	87.6	0.64		
Ailurus	58.3	95	0.61	25	0.43
Martes	32	56.5	0.56		
Canis	55	88.5	0.64	26.2	0.47

Jenkins 1983). *Barunlestes*, a Late Cretaceous eutherian from Mongolia, also has long and slender ilium (Kielan-Jaworowska 1978) although apparently not longer than in *Mayulestes*. A long and narrow ilium is also present in *Asiatherium* (Szalay & Trofimov 1996). It seems therefore that a long and narrow ilium could represent the plesiomorphic condition of the mammalian ilium. Considering the morphology of the ilium of *Mayulestes*, longer than that of the younger borhyaenoids, it is likely that early history of the superfamily is characterized by a shortening of the ilium. A long and slender ilium seems to be fairly constant in early mammals, which would indicate that it represents the plesiomorphic condition. Furthermore, such a morphology of the ilium is by far the most common one within marsupials. The short ilium of *Pucadelphys* would hence be specialised compared to that of the living didelphids. However, skeletons of Late Cretaceous or Palaeocene marsupials are too scarce to provide adequate comparison and, so far, it seems difficult to answer this question.

Mayulestes and *Pucadelphys* have conspicuously everted iliac wings contrary to the condition observed in the living didelphids and phalangerids which have relatively straight and narrow wings. An important extroversion of the wing of the ilium is found in some cursorial (thylacine, canids, most ungulates), fossorial [wombat, bandicoots (also cursosaltatorial), aardvark, badgers, ratel], aquatic (phocids, walrus, sea otter) and arboreal mammals [koala, phalanger, small and giant panda, arboreal tree shrews, squirrels, lemurs, indri, spider monkey (the five latter, capable of powerful leaping)]. In the phalangerids, the iliac wings are slightly everted at their apices. Bears and anteaters also have everted iliac wings. In *Cladosictis* and *Prothylacynus*, two borhyaenoids from the middle Miocene of the Santa Cruz beds (Argentina) the eversion of the ilium is comparable to that of *Mayulestes*. On the medial side of the wing of the ilium the erector spinae is inserted (consisting of the iliocostalis and longissimus muscles), a powerful extensor of the vertebral column. The origin of this muscle is on the dorsal side of the thoracic and lumbar vertebrae and ribs. An everted ilium, therefore, leaves more space to the posterior portion of the erector spinae at the angle between the vertebral column and the pelvis and denotes that this muscle was powerful in *Mayulestes*, as in *Cladosictis* and *Prothylacynus*. The same can be said for *Pucadelphys*. On the lateral side of the iliac wing are the origins of the glutei medius and superficialis, muscles inserted on the tip of the greater trochanter (gluteus medius) and, more distally, on the lateral side of the greater trochanter (gluteus superficialis). An everted ilium allows for more space for the gluteus medius and superficialis (and a greater muscular mass) than in an animal with a non-everted ilium as is the case in living didelphids. Other muscles originating on the anteroventral region of the ilium are the sartorius and tensor fascia lata. These muscles are inserted on the patella and are flexors of the hip and/or extensors of the leg. An everted ilium gives more power to these muscles since it increases the lever arm of their action. The morphology of the wing of the ilium of *Mayulestes* therefore indicates a more important activity of the vertebral column and coxofemoral articulation than in the living didephids. The epaxial musculature mentioned above contributes to the propulsive stroke of the hind limb with vertical or horizontal (as in seals and walruses) movements of the vertebral column. Those movements can occur in all the ecotypes mentioned above. In the case of the arboreal ecotypes (as noted above, *Mayulestes* has several features of its forelimb that can interpreted as arboreal), eversion of the iliac wing can be due to leaping (lemurs, indri, spider monkey), to leaping run [tree shrews (Jenkins 1974), squirrels], or to a vertical climbing position as observed in koalas and sometimes in cuscuses. Living didelphids which generally (when unstressed) do not move very fast, which walk on the branches with the help of their grasping manus and pes and which are not jumpers, do not have an everted ilium. The only living didephid which has an ilium slightly more everted than the other ones is the terrestrial genus *Metachirus*. This is probably related to the terrascansorial (Szalay 1994) mode of terrestrial locomotion of the brown four-eyed opossum, which is extremely agile on the ground and whose locomotion is a sort of leaping run (Charles-Dominique pers. comm.). It is note-

worthy that the Plio-Pleistocene saltatorial marsupial *Argyrolagus* has an everted ilium (Simpson 1970). Therefore, the eversion of the ilium of *Mayulestes* probably denotes some leaping or bounding ability.

The anteroventral iliac spine of *Mayulestes* is clearly deflected ventrally as in *Cladosictis* and *Prothylacynus* (but to a lesser extent). Among living didelphids the only form which shows an anteroventral iliac spine slightly deflected anteroventrally is the terrascansorial *Metachirus*. On the medial side of the anteroventral region of the iliac wing is inserted the quadratus lumborum, an important flexor of the vertebral column. This muscle was hence powerful in *Mayulestes*. This condition is in agreement with the large transverse processes of the lumbar vertebrae (where the muscle originates) and with the inferred strength of the erector spinae (the antagonist muscle of the quadratus lumborum and psoas minor). On the anteroventral iliac spine the obliquus abdomini internus was also probably inserted, as in many other marsupials (Elftman 1929). This muscle is another flexor of the trunk. Flexion of the vertebral column is an important movement in cursorial and saltatorial mammals and acts in synergy with the recovery stroke of the hindlimb when the animal is running or leaping (Elftman 1929). The fact that the anteroventral iliac spine of *Mayulestes* is relatively more developed than in the arboreal didelphids indicates that, although certainly not cursorial, it was probably capable of relatively fast running (probably for a relatively short distance) and/or some bounding. The greater development of this spine in *Cladosictis* and *Prothylacynus* is indicative of some cursorial ability (probably for short distances) in those Santacruzian forms and, very probably, bounding in order to seize their prey by surprise. This morphology of the anteroventral angle of the iliac wing is also present in the cursosaltatorial (but also partly fossorial) *Perameles* and in the superfossorial *Orycteropus*. However, since it is absent in other fossorial mammals (wombat, fossorial rodents, armadillos, meline mustelids, giant anteater) it is probably not related to digging. Although capable of a relatively fast gallop when chased (Novak & Paradiso 1983), *Orycteropus* is certainly not a cursorial animal. No interpretation is given here of the ventrolaterally deflected anteroventral iliac spine of *Orycteropus*. In *Perameles* it is probably related to the pronounced leaping and running ability of this animal.

It has been shown above that *Mayulestes* bears several features that can be related to arboreality. Therefore, if this interpretation is correct, the everted ilium and the well-developed anteroventral iliac spine of *Mayulestes* could be interpreted as indicating some running and/or leaping ability, perhaps approaching the extremely fast and agile leaping run of tree shrews and squirrels but certainly not as fast. Marshall & Sigogneau-Russell (1995: 150) have suggested that *Pucadelphys* had both leaping and digging ability. Since the scapula and the caudal vertebrae of *Pucadelphys* have been shown to have characters compatible with arboreality (shape and position of the acromion and prehensile tail), an interpretation similar to that of *Mayulestes* could be given for the everted ilium and the ventrally deflected anteroventral iliac spine of *Pucadelphys*. They are therefore preferentially related here to leaping rather than digging function.

The tuberosity for the rectus femoris is slightly larger in *Mayulestes* than in the living didelphids. However, it is much smaller than in *Cladosictis* and *Prothylacynus*. A well-developed tuberosity for the rectus femoris is found in peramelids, sciurids, tupaiids, canids, leporids, aardvark, giant anteater, some fossorial and some terrestrial rodents, lemurs, indri, *Argyrolagus*, *Pucadelphys* and *Barunlestes*. The rectus femoris is a powerful extensor of the knee and a flexor of the hip. It is an efficient actor during the stroke (if the extensors of the hip prevent it from flexion) and during the recovery phase. A powerful rectus femoris is an important advantage to increase the power and strength of the stroke. The need for a powerful stroke of the hindlimb is easily understandable in a fast runner, in a jumper or in very agile and active small mammals (arbo- or terrascansorial). It is also essential in an animal which needs to be able to escape very quickly (because of predators or any kind of social behaviour). In *Mayulestes* the relatively small rectus femoris (only slightly larger than in the living didephids)

would indicate a much less active animal than a tree shrew or a squirrel but, a little more than in the living didelphids. On the contrary, *Pucadelphys*, with a well-developed tuberosity, probably had a stronger rectus femoris than in the living didelphids which could be related to an important agility possibly as is observed in squirrels or tupaiids. In *Cladosictis* and *Prothylacynus* which are much larger animals, the inferred large size of the rectus femoris tuberosity could be related to bounding ability, an action used by non-cursorial predators which lie in wait and which is generally combined with fast but short run.

The ischiatic tuberosity of *Mayulestes* is smaller than in the Santa Cruz borhyaenoids and most living didelphids. It approaches the size of that of *Caluromys*. A well-developed ischiatic spine is found in cursorial (thylacine, canids, most ungulates, *Dolichotis*), cursosaltatorial and saltatorial (lagomorphs, dipodids rodents), fossorial (wombat, marsupial mole, aardvark, geomyids, bathyergids, meline mustelids), aquatic (sea otter, seals, walrus) and arboreal mammals [koala, lemurs, indri, avahi (although less developed in those forms than in those mentioned above)]. Bears also have a large ischiatic tuberosity, probably related to their capacity for bipedality (occasionally and for short distances). Among Recent mammals the better developed ischiatic tuberosities are found in cursorial and highly fossorial mammals. In the other Recent mammals the development is generally not so spectacular. However, a reasonably well-developed ischiatic tuberosity is present in some arboreal mammals (phalangerids, *Dendrolagus*, sciurids, tupaiids). In other respects, it is noteworthy that, in the living didelphids, the ischiatic spine is generally more developed in the terrestrial and arboreal-terrestrial forms than in the strictly arboreal forms. Among fossil mammals, North American (arboreal) and Asiatic (terrestrial) multituberculates have a well-developed ischiatic tuberosity (respectively, Krause & Jenkins 1983; Kielan-Jaworowska & Gambaryan 1994); it does not seem to be well-developed in *Henkelotherium* (Krebs 1991); it is weak but salient in *Gobiconodon* (Jenkins & Schaff 1988) and rounded in *Megazostrodon* (Jenkins & Parrington 1976). Therefore, the reduced size of the ischiatic spine of *Mayulestes* indicates that it was certainly not cursorial nor fossorial. Its condition is not incompatible with arboreal life but does not particularly reinforce this hypothesis.

The ischium of *Mayulestes* is relatively long when compared to those of living didelphids (Table 7). However, its relative length is compatible with that observed in *Cladosictis* and *Prothylacynus*. As shown in table 7 the length of the ischium is quite variable in the same ecotype. For instance, fossorial mammals are considered to have a long ischium. This is obviously true for the super-digger *Orycteropus* but not for the geomyid or bathyergid rodents. Leaping mammals also have generally long ischia (allactaga, kangaroo). The benefit of a long ischium is an increase of the lever arm of the extensor muscles of the hip and knee (biceps femoris, semimembranosus, semitendinosus, quadratus femoris) and therefore a more powerful extension of the hind limb essential in digging and leaping. In tupaiids and peramelids the ischia are similar in size to those of *Mayulestes* and *Pucadelphys* (Table 7). Tupaiids and peramelids are extremely active and dynamic

TABLE 7. — Relative length of the ischium in various marsupials and placentals. **Lis**, length of the ischium; **Lt**, total length of the innominate. All measurements are in millimeters.

	Lis	Lt	Lis/Lt
Mayulestes (MHNC 1249)	17.7	43.5	0.4
Cladosictis (YPM PU 15170)	37	101.5	0.36
Cladosictis (YPM PU 15702)	47	123	0.38
Prothylacynus (YPM PU 15700)	81e	184 e	0.44
Pucadelphys (YPFB Pal 6106)	10	24	0.41
Didelphis	22	75	0.29
Metachirus	12.5	40	0.31
Monodelphis	8	25	0.32
Marmosa	5	17.5	0.28
Caluromys	14.5	45	0.32
Phalanger	23	70	0.32
Sciurus	18	49	0.36
Tupaia	11.5	30	0.4
Ailurus	31	93	0.33
Perameles	35	86	0.4
Orycteropus	150	260	0.57
Geomys	14	46	0.3
Bathyergus	20	47	0.42
Allactaga	23	45	0.51
Argyrolagus	14.5	38	0.38

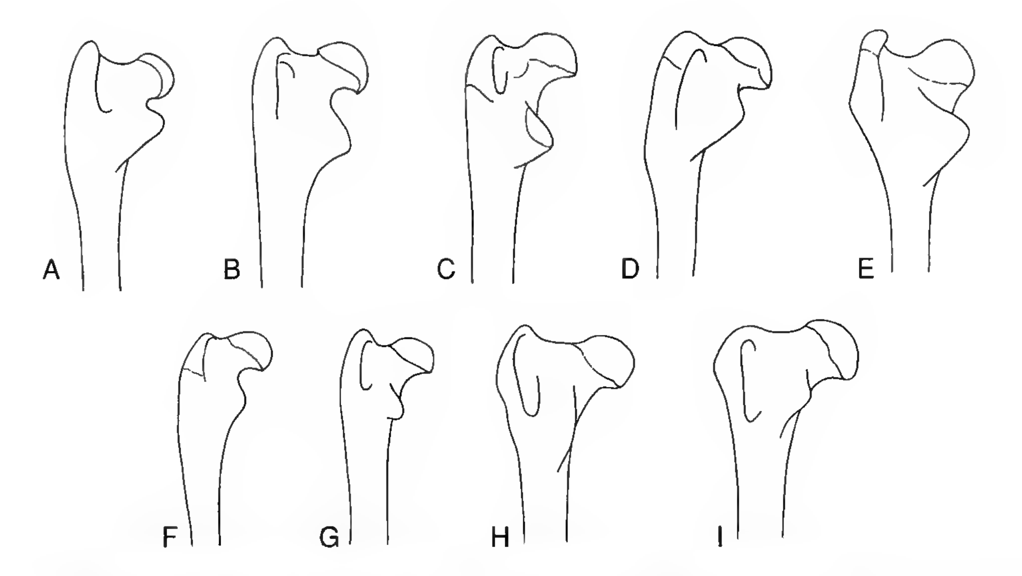


FIG. 53. — Posterior view of the proximal third of the left femur in several marsupials: **A**, *Mayulestes*; **B**, *Caluromys*; **C**, *Didelphis*; **D**, *Pucadelphys*; **E**, *Phalanger*; **F**, *Monodelphis*; **G**, *Metachirus*; **H**, *Borhyaena*; **I**, *Prothylacynus*. Not to scale.

mammals and the morphology of the ischia of *Mayulestes* and *Pucadelphys* could simply be related to their agility (*Perameles* is also partially fossorial). However, the fact that tamanduas have the same ratio "length of the ischium/total length of the pelvis" as squirrels indicates that the interpretation of this feature is perhaps not as simple as it appears at first.

Coxofemoral articulation. The relatively open acetabulum of the pelvis of *Mayulestes* indicates a good mobility of the hip to a degree comparable to that observed in the most arboreal didelphids and in the Australian phalangerids. As in the latter the thickened and elevated anterior border of the acetabulum provides a good anterior buttressing system of the hip articulation. The concave dorsal border (in dorsal view) of the acetabulum provides a greater amplitude of abduction (and in part of inversion) of the femur which allows a better opening of the legs and gives more stability in the case of an arboreal animal. On the contrary this condition would be a handicap in the case of a terrestrial cursorial animal where the movements of the limbs tend to be parasagittal (Kappelman 1988). It is therefore probable that *Mayulestes* had a relatively more mobile articulation of the hip and greater ability to have the legs widely spread than *Cladosictis* and *Prothylacynus*. The condition of *Mayulestes* was probably approaching that of arboreal marsupials such as didelphids and phalangerids. It is noteworthy that a similar structure of the acetabulum is found in *Eozostrodon*, interpreted as partially arboreal by Jenkins & Parrington (1976). Among living forms it is present in tupaiids, in most arboreal didelphids, in phalangerids and petaurids. Kielan-Jaworowska & Gambaryan (1994: 70) note that: "Elftman (1929) stated that the acetabulum is open dorsally in arboreal didelphids and *Pseudochirus*". However, Elftman (1929: 223) actually stated: "In arboreal forms, such as *Didelphys* (sic) and *Pseudochirus*, the cup is more opened allowing greater freedom of movement of the head of the femur". Elftman (1929: 225) also stated that "the acetabulum of *Petauroides* is somewhat more open than that of *Pseudochirus*" and "in *Petauroides* the acetabulum has a deeper notch dorsally than in *Pseudochirus* allowing extreme abduction of the femur during gliding." In fact the acetabulum is never totally open dorsally but its dorsal border is more concave (in dorsal view) in arboreal forms (*Caluromys*, *Caluromysiops*) and terrestrial-arboreal forms (*Didelphis*) than in strictly terrestrial forms (*Metachirus*).

On the proximal extremity of the femur, the tro-

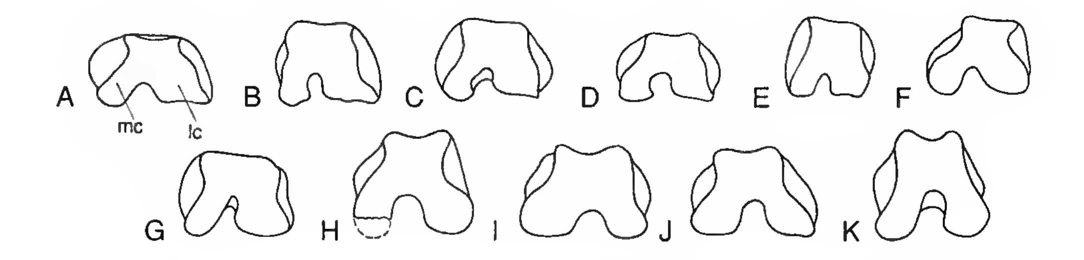


Fig. 54. — Distal view of the distal epiphysis of the right femur in several marsupials: **A**, *Caluromys*; **B**, *Didelphis*; **C**, *Philander*; **D**, *Monodelphis*; **E**, *Metachirus*; **F**, *Pucadelphys*; **G**, *Phalanger*; **H**, *Mayulestes*; **I**, *Borhyaena*; **J**, *Prothylacynus*; **K**, *Thylacinus*. Abbreviations: **lc**, lateral condyle; **mc**, medial condyle. Not to scale.

chanters are well-developed and expanded in the plane of the epiphysis. The size of the trochanters of *Mayulestes* is similar to that observed in phalangerids, slightly greater than in the living didelphids and much more developed than in the Santa Cruz borhyaenoids. Among the living didephids, the trochanters are more developed in the arboreal forms (*Caluromys*, *Didelphis*, *Philander*). In the terrestrial forms (*Metachirus*, *Monodelphis*) their relative size varies. In *Metachirus* the greater trochanter is relatively high (probably in relation to the leaping ability) while in *Monodelphis* the greater trochanter is smaller than in other didelphids, although the lesser trochanter is relatively well-developed (Fig. 53). The development of the trochanters of *Mayulestes* corroborates the great mobility of the coxofemoral articulation suggested by the morphology of the acetabulum.

The morphology of the coxofemoral articulation and the proximal extremity of the femur of *Pucadelphys* are very similar to those of *Mayulestes* except a slightly deeper acetabulum and a slightly lower greater trochanter in the former. As in *Mayulestes*, the morphology of the acetabulum and proximal extremity of the femur of *Pucadelphys* suggests a well-developed mobility and power of the coxofemoral articulation and is consistent with some arboreality.

Femorotibial articulation. The distal epiphysis of the femur of *Mayulestes* is anteroposteriorly longer than that of the Didelphidae and that of the Santa Cruz borhyaenoids (Fig. 54, Table 8). *Caluromys*, the most arboreal didelphid, has the most anteroposteriorly flattened distal epiphysis of the femur while the most quadrate (in distal view) is found in *Metachirus* which is exclusively terrestrial. Between these two poles are several intermediate types of totally or partially arboreal genera. Phalangerids also have an anteroposteriorly flattened distal epiphysis of the femur. A flattened distal epiphysis of the femur seems therefore related to arboreality in didelphids. However, the distal extremity of the femur is not flattened in *Tupaia*, *Sciurus*, *Nasua*, *Ailurus*, although it is so in *Potos*. Therefore, an arboreal mode of life does not always implies the presence of a flattened distal epiphysis of the femur and the proportions of the distal epiphysis of the femur of *Mayulestes* (which are closer to those of *Metachirus* than to those of *Caluromys*) do not to argue against arboreal adaptation. An anteroposteriorly elongated distal epiphysis of the femur indicates a greater amplitude of the movements of the knee which could be related to some running or leaping ability. Highly cursorial canids and thylacinids and saltatorial kangaroos or indris have a very triangular distal epiphysis of the femur. As a matter of fact the terresrrial *Metachirus* is a very active runner which shows good leaping ability and whose distal epiphysis of the femur is much longer anteroposteriorly than in the other living didelphids. Therefore, the proportions of the distal epiphysis of the femur would be more informative on the way of locomotion than on the habits (arboreal *vs* terrestrial). The morphology observed in *Mayulestes* could possibly indicate a relatively more agile animal than the living didelphids, capable of some running and/or some bounding or leaping ability.

The distoproximal elevation of the femoral trochlea, its depth and its salient crests, when compared to the living didelphids, suggest more stress in the articulation which would be in agreement with more powerful and faster movements. During fast movement a deeper trochlea is necessary for a better guiding of the tendon of the vasti and rectus femoris (which inserts on the tibial tuberosity) and to prevent it from dislocation. Living didelphids and cuscuses which have a shallow femoral trochlea are relatively slow movers (although some didelphids are faster than others, i.e. *Metachirus*). Extremely fast saltatory runners (squirrels and tree shrews), cursorial mammals, arboreal jumpers primates (*Tarsius*, galagos, lemurs, cheirogaleids indriids) and saltatorial rodents (dipodids, pedetids, some gerbillids) generally have a well-marked, proximodistally elongated femoral trochlea with relatively elevated crests. As mentioned by Tardieu (1983), a deep and long trochlea with elevated crests is fundamental in jumping primates and allows better retention of the patella in its articular position during extension. A well-marked trochlea seems to be related to fast movements. Slow climbers such as lorisines primates have a wide and flat trochlea as seen in didelphids and phalangerids. However, the slow moving tamanduas and pangolins have a very deep trochlea with very elevated crests and the extremely fast squirrels and tree shrews do not have a more pronounced trochlea than the relatively slow moving lesser panda. Hence, the significance of the femoral trochlea is not clear. Within the borhyaenoids, *Mayulestes* resembles *Cladosictis* in having a well-marked trochlea but not as deep as in the fast moving jumping lemuriforms mentioned above. *Borhyaena* and *Prothylacynus* which have short and shallow femoral trochleae were certainly not as highly cursorial as a thylacine. Therefore, when compared with living didelphids, the morphology of the trochlea of *Mayulestes* would indicate a more agile animal probably capable of some running and/or leaping, although, as mentioned above, this feature is not as reliable as is often believed.

The femoral trochlea of *Mayulestes* is strongly asymmetrical and the lateral lip is much more elevated than the medial one. Furthermore, the lateral side of the trochlea extends more proximally on the anterior face of the diaphysis than the medial side. This is probably related to the size of the lateral condyle which is much larger than the medial one. An interesting comparison can be made with the femur of *Tamandua*, where the medial condyle is the largest and where the medial crest of the trochlea is much stronger and much more elevated than the lateral one. Thus, a relation seems to exist between the size of one distal femoral condyle and the development of the corresponding crest of the femoral trochlea. The elevation of the lateral lip of the femoral trochlea corresponds to a necessity to prevent the joint from dislocation, more important on the lateral side of the joint than on the medial one. In *Didelphis* the average position of the femur when the animal is walking is close to horizontal, the knee being slightly lower than the hip (Jenkins 1971). In this position, a slight dorsoventral (anticlockwise for the left femur and clockwise for the right one) rotation of the femur on its axis will place the lateral lip of the trochlea below the medial lip. Such a position would imply the necessity for a stronger lateral lip of the trochlea in order to maintain the patella (or the vastus tendon, if there was no patella) in the trochlear groove. A dorsoventrally rotated

TABLE 8. — Proportions of the distal epiphysis of the femur in various marsupials. L, length; W, width. All measurements are in millimeters.

	W	L	L/W
Mayulestes (MHNC 1249)	7.9	6e	0.76
Cladosictis (YPM PU 15170)	21.5	17	0.79
Prothylacynus (YPM PU 15700)	42	31	0.74
Borhyaena (YPM PU 15701)	36	26.7	0.74
Thylacinus	32.5	30.5	0.93
Pucadelphys (YPFB Pal 6105)	4.8	3.3	0.68
Pucadelphys (YPFB Pal 6106 left)	4.8	3.6	0.75
Pucadelphys (YPFB Pal 6106 right)	4.9	3.7	0.75
Pucadelphys (YPFB Pal 6110)	4.5	3.2	0.71
Caluromys	9.5	5.5	0.58
Didelphis	13.7	9.5	0.69
Philander	10.3	7.2	0.7
Marmosa	2.5	1.9	0.76
Monodelphis	4.5	3.2	0.71
Metachirus	7	6	0.85
Phalanger	14.2	10.5	0.73

position of the femur will have the effect of adducting the crus. The utility of an adducted position of the crus is easily understandable in an arboreal (arboscansorial) animal which would climb grasping the branches laterally (or dorsolaterally) as the living didelphids or tupaiids do (Jenkins 1974, 1984). Therefore, considering the position of the femur, the morphology of the femoral trochlea of *Mayulestes* can be interpreted as related to arboreality in the case of a didelphid-like or tupaid-like climbing strategy (see below) but was probably associated to fast and powerful movements.

Another major feature of the tibiofemoral articulation of *Mayulestes* is the relative width of the distal condyles (Fig. 54, Table 9). As in didelphids and phalangerids, the medial condyle is much narrower than the lateral one, while the contrary is observed in the Santa Cruz borhyaenoids. The didelphid condition varies according to the habits of the species. The most significant difference in the width of the condyles is observed in *Caluromys*, the most arboreal didelphid, while in *Metachirus*, a terrestrial genus (Janson & Emmons 1990), the medial condyle is wider and the lateral condyle narrower than in *Caluromys* but the former is still clearly narrower than the latter. Therefore, it seems that, among didelphids, the degree of arboreality is inversely proportional to the relative width of the medial condyle of the femur (*i.e.* the most arboreal, the narrowest). In *Mayulestes*, the relative size of the medial condyle (WM/WL 0.73) is close to that of *Metachirus* (WM/WL 0.75). It is, however, much smaller than in the Santa Cruz borhyaenoids (WM/WL varies from 0.95 to 1.2) and it is closer to the most arboreal didelphid (*Caluromys* WM/WL 0.48) than to *Borhyaena* and *Cladosictis*. It is noteworthy that *Eozostrodon*, a genus interpreted as partially arboreal, has a lateral condyle of the femur which approximately twice the size of the medial condyle (Jenkins & Parrington 1976). The distal condyles of the femur are generally subequal in width in the essentially terrestrial *Caenolestes* and in the cursosaltatorial *Perameles*. In *Ptilodus*, *Stygimys*, ? *Mesodma* and ? *Eucosmodon*, arboreal multituberculates from North America (Krause & Jenkins 1983: 221, figs 19B, 20E, 21E), the lateral condyle of the distal epiphysis is wider than the medial condyle, while in *Chulsanbaatar*, a terrestrial multituberculate from the Gobi Desert (Kielan-Jaworowska & Gambaryan 1994: fig. 17), both condyles are subequal in width; in *Kryptobaatar*, another terrestrial multituberculate from the same region (Kielan-Jaworowska & Gambaryan 1994: 12), the medial condyle is wider than the lateral one. It seems, therefore, that narrowing of the medial distal condyle of the femur could be related to some kind of arboreality. The precise function of that peculiar morphology has not been elucidated. However, it is noteworthy that it is present in several non-therian mammals [*Eozostrodon*, *Erythrotherium*, *Megazostrodon*, *Ptilodus*, *Stygimys*, ? *Mesodma*, ? *Eucosmodon*, *Henkelotherium* (apparently, from Krebs 1991: fig. 11, pl. 3)]. In placental mammals, when distal condyles of the femur do not have the same width, the narrowest is always the lateral condyle. Therefore, the presence of a medial condyle conspicuously narrower than the medial one could represent a plesiomorphy. *Mayulestes* would thus retain the plesiomorphic condition within mammals.

The medial femoral condyle articulates, on the tibia, with a reniform, elongated and concave (almost grooved in *Caluromys*, *Didelphis* and

TABLE 9. — Relative width of the distal femoral condyles in marsupials. **Wl**, width of the lateral condyle; **Wm**, width of the medial condyle. All measurements are in millimeters.

	Wl	Wm	Wm/Wl
Mayulestes (MHNC 1249)	3.13	2.3	0.73
Cladosictis (YPM PU 15702)	10.2	11	1.07
Borhyaena (YPM PU 15701)	12.5	17	1.2
Prothylacynus (YPM PU 15700)	16	15.2	0.95
Caluromys	3.9	1.9	0.48
Philander	4.2	2.3	0.54
Didelphis	6.4	3.8	0.59
Marmosa	1.28	0.67	0.52
Phalanger	7.2	4.3	0.59
Monodelphis	1.8	1.5	0.83
Metachirus	2.9	2.2	0.75
Pucadelphys (YPFB Pal 6106)	2.4	1.8	0.75
Pucadelphys (YPFB Pal 6105)	2	1.5	0.75
Pucadelphys (YPFB Pal 6110)	2.1	1.6	0.76

Phalanger) medial tibial facet which indicates anteroposterior movements and some rotational ability of the femorotibial articulation (Jenkins & Parrington 1976: 424). The lateral facet is wider, roughly quadrate and convex or flat and probably received the axis of rotation (Jenkins & Parrington 1976: 428). Cineradiographic studies have demonstrated the necessity for such a rotation during the representative phases of the walking step in *Didelphis* (Jenkins 1971). It is likely that rotation movements of the knee are useful too in climbing, in order to help the inversion of the foot while grasping the branch on which the animal is moving (see below). However, Jenkins & McLearn (1984: 216) noted that there is no significant contribution of femorotibial rotation to foot reversal. Although less pronounced than in *Caluromys* or *Didelphis*, the condition of *Mayulestes* clearly indicates some capacity for rotation of the knee. A similar femorotibial articulation is also found in *Pucadelphys*, although less developed than in most living didelphids.

On the proximal epiphysis of the tibia, the tibial tuberosity is not protruding anteriorly in *Mayulestes*, didelphids, phalangerids and *Phascolarctos*. As a consequence, the epiphysis is flattened anteriorly and does not have the triangular shape observed in the Santa Cruz borhyaenoids and in highly specialised cursorial (thylacinids, canids, felids, ungulates) and terrestrial saltatorial (kangaroos, rabbits, pedetids) mammals (Fig. 55, Table 10). The development of the tibial tuberosity indicates the importance of traction exerted on the patellar ligament or (if there is no patella, as in didelphids) on the conjoined tendon of the vasti and rectus femoris. The action of these muscles is a powerful extension of the leg, an essential movement in fast-running and jumping animals. On the contrary, rapidity and power of this movement is less important in the relatively slow-moving arboreal didelphids. In *Metachirus*, a terrestrial didelphid regarded by Szalay (1994) as subcursorial, the tibial tuberosity is more developed than in the highly arboreal *Caluromys* and the proximal epiphysis of the tibia is clearly triangular, while it is anteroposteriorly flattened in *Caluromys* and *Mayulestes*. In fact, in didelphids there is a gradient of the shape of the proximal epiphysis of the tibia from reniform in *Caluromys* (the most arboreal didelphid) to clearly triangular in *Metachirus* (a terrestrial didelphid). In *Didelphis* and *Philander*, both terrestrial-arboreal genera, the morphology of the proximal epiphysis is intermediate. In *Dendrolagus*, the arboreal kangaroo, the tibial tuberosity is much less developed than in the terrestrial macropodids. An anteroposteriorly flattened proximal epiphysis of the tibia is also found in several slow moving arboreal eutherians (*Potos*, *Ailurus*, *Tamandua*, *Choloepus*, *Bradypus*). It seems that the faster the animal is moving, the more triangular the epiphysis will be. For instance, the fast-moving squirrels have a more triangular epiphysis than *Potos* or *Bradypus*, but do not have the anterior protrusion of the tibial tuberosity observed in a cursosaltatorial rabbit. Therefore, the morphology of the proximal epiphysis of *Mayulestes* would indicate relatively slow movements, which contrasts with the relative agility suggested by the anatomy of other elements of the postcranial skeleton (pelvis). However, the interpretation of that feature is probably more complex since, in the extremely agile and fast tupaiids, the proximal epiphysis of the tibia is relatively short anteroposteriorly while the distal epiphysis of the femur is not anteroposteriorly flattened. Furthermore, the saltatorial lemuriforms (indris, galagos, lemurs) have an anteroposteriorly short proximal extremity of the tibia associated with an anteroposteriorly long distal epiphysis of the femur, with a

TABLE 10. — Comparison of the proportions of the proximal epiphysis of the tibia in marsupials. L, anteroposterior length; W, transverse width. All measurements are in millimeters.

	L	W	L/W
Mayulestes (MHNC 1249)	5.4	7.8	0.69
Cladosictis (YPM PU 15046)	19.1	19.7	0.97
Prothylacynus (YPM PU 15700)	36	39.5	0.91
Thylacinus	33.5	29	1.15
Caluromys	7.7	8.5	0.905
Didelphis	11.3	12.2	0.926
Metachirus	7.2	7.6	0.94
Monodelphis	3	3.9	0.77
Phalanger	9.2	10.3	0.89
Potos	14.8	18.5	0.8

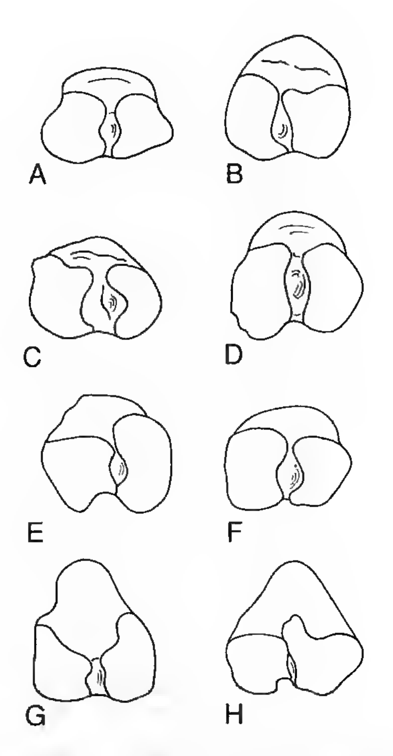


Fig. 55. — Proximal view of the right tibia in several marsupials: **A**, *Mayulestes*; **B**, *Didelphis*; **C**, *Caluromys*; **D**, *Metachirus*; **E**, *Phalanger*; **F**, *Phascolarctos*; **G**, *Thylacinus*; **H**, *Prothylacynus*. Not to scale.

deeply grooved trochlea. Therefore, the morphology of the proximal epiphysis of the tibia of *Mayulestes*, which is similar to that of the saltatorial lemuriforms mentioned above, could indicate some saltatorial ability. The combination of an anteroposteriorly long distal femur with an anteroposteriorly short proximal tibia is also found in several terrestrial cercopithecids (macaque, baboon) which are very agile and, occasionally, good runners. The relative anteroposterior length of the distal epiphysis of the femur and the shortness of the proximal epiphysis and articular facets of the tibia would indicate that the tibial condyles can have an long trajectory on the femoral condyles, which denotes capacity of a significant amplitude of the movements of the knee as in saltatorial lemuriforms. It is therefore perhaps not incompatible with an agile and a relatively fast-moving animal. The morphology observed on the tibia of *Prothylacynus* and, to a lesser extent, *Cladosictis*, with a well-developed tibial tuberosity, would denote some cursoriality and bounding ability.

Diaphysis of the tibia. The well-marked characteristic sigmoid morphology of the shaft of the tibia (in anterior view) of *Mayulestes* (proximal third to half, bowed laterally; distal half to two thirds, bowed medially) is found in all living didelphids and to a lesser extent in *Dasyurus*, *Petaurus*, *Sminthopsis*, *Acrobates*, *Pseudochirus* and *Dendrolagus*, all arboreal or partially arboreal marsupial genera. A sigmoid tibia is also found in *Caenolestes* and *Sarcophilus*, both mainly terrestrial but capable of climbing and in some cases very agile (Novak & Paradiso 1983). *Eozostrodon*, an arboreal form according to Jenkins & Parrington (1976), also has a sigmoid tibia. The tibiae of the terrestrial Mongolian multituberculates *Chulsanbaatar*, *Kryptobaatar* and *Nemegtbaatar* are not sigmoid, but, straight, slightly bent laterally and strongly bent laterally respectively (Kielan-Jaworowska & Gambaryan 1994), while those of the arboreal North American genera *Ptilodus* and ? *Mesodma* are sigmoid (Krause & Jenkins 1983). The tibia of *Henkelotherium*, regarded as a partially arboreal eupantothere, is also slightly sigmoid (Krebs 1991). However, the tibiae of *Pucadelphys*, *Phalanger* and *Phascolarctos*, are straight. The tibia of cynodonts is strongly bent laterally but not sigmoid. The sigmoid morphology of the tibia is probably due to highly variable direction of the various tensions exerted on the bone in the case of an arboreal form. In cursorial mammals the direction of forces is probably more parallel to the main axis of the bone, whose straightness increases its mechanical resistance. Furthermore, the distribution of that feature among the multituberculate genera cited above would be indicative of a relation to some climbing ability. If this interpretation is correct, its absence in the koalas and phalangers is probably due to a different type of arboreal locomotion in these genera. It is noteworthy that the tibia of *Cladosictis*, *Prothylacynus* (probably both with some cursorial ability, *i.e.* terrascansorial) and *Thylacinus* (definitely cursorial) is straight. The presence of a very sigmoid tibia in *Mayulestes* certainly confirms its lack of cursorial adaptation and probably reinforces the hypothesis of arboreality. Nevertheless, biomechanical studies are

needed to confirm the relationships of a sigmoid tibia to arboreality.

Astragalotibial articulation. The upper ankle joint is important in understanding locomotory habits. The astragalus of *Mayulestes* is unknown, however, the morphology of the astragalar facets of the tibia are highly informative. As noted above, the flattened malleolus is oriented at an angle of 135° with the transverse axis of the tibial condyles. A consequence of this morphology is that an extension of the upper ankle joint will automatically result also in an inversion and the sole of the foot which will tend to face posteromedially. In *Prothylacynus*, *Cladosictis* and *Thylacinus*, since the malleolus is approximately parallel to the transverse axis of the tibial condyles, an extension of the foot will orientate the sole posteriorly. In didelphids, phalangerids and petaurids, the lateral tibioastragalar facet is helical and an extension of the foot is also accompanied by an inversion. Didelphids are known for having very prehensile hands and feet capable of efficient hallucial grasping (except, probably, the hind foot of *Chironectes*, the aquatic didelphid). The same is true in phalangerids and petaurids. Figure 13 of Jenkins & McLearn (1984) (which is based on photographs) well illustrates how *Didelphis* walks on a branch. The hands and feet tend to grasp the branch laterally or dorsolaterally which constrains the animal to have its hands and feet facing, at least partially, medially. Another very demonstrative figure is that of Novak & Paradiso (1983: 24, top photograph) where the right hindfoot of a *Caluromysiops* standing on a branch, is extended and faces medially grasping the branch, the hallux being above and the other digits lateral (Novak & Paradiso 1983: 13, 61, 64-66, 68, 70). I have made the same observation on *Caluromys* in captivity; in this genus grasping is also often achieved with digits I and II above the branch and digits III, IV and V, below. A similar grasping of the branch is also observed in *Tupaia*, although locomotion is much faster than in didelphids. Jenkins (1974: 98) states that "when running at maximum speed on small branches *Tupaia glis* supinates each manus as much as 90°. As the contact of both hands is nearly synchronous, the effect is to grip the branch between the right and left manus rather than to run on the top of it". The same is observed on the foot which is also abducted and inverted (Jenkins 1974) when walking on branches less than 2 cm in diameter. Considering the shape of a branch, the position of the hands and feet during didelphid and tupaid arboreal locomotion appears to be obvious. So are the modifications of the upper ankle joint movement and articulation. Therefore, the morphology of the distal extremity of the tibia of *Mayulestes* and the resulting inferred movements of the ankle are in agreement with a didelphid type of arboreal locomotion, although morphologically different. In *Pucadelphys* the malleolus is also at an angle of more than 90° with the transverse axis of the tibial condyles. Furthermore, in this genus, the lateral tibioastragalar facet is slightly helical, although less than in living didelphids. These features represent an indication of capacity of inversion of the foot during extension of the lower ankle joint and ability of hindfoot reversal as is observed in living didelphids and many other arboreal marsupials and placentals (Jenkins 1974). The morphology of the astragalotibial articulation of *Pucadelphys* is therefore indicative of arboreality. Since the astragalus of *Mayulestes* is unknown, it is not possible to confirm the reversal ability (Jenkins & McLearn 1984) suggested by the astragalar facets of the tibia.

Calcaneum. The calcaneum of *Mayulestes* also provides important information on the movement of the lower ankle joint. The ectal and sustentacular facets strongly face medially, while in *Sipalocyon* they face mainly dorsally and slightly distally (Fig. 56). In living didelphids and phalangerids the ectal and sustentacular facets also face mainly medially but to a lesser extent than in *Mayulestes*; the medial orientation is more pronounced in *Caluromys* and *Marmosa* than in *Didelphis* and *Metachirus*. The morphology observed in *Sipalocyon* is obviously related to plantigrady. In that case, the astragalus directly receives the weight of the body through the tibioastragalar articulation with reduced shearing forces (tangential forces). The weight of the animal is transmitted to the calcaneum through the ectal and sustentacular facets. Therefore, the arti-

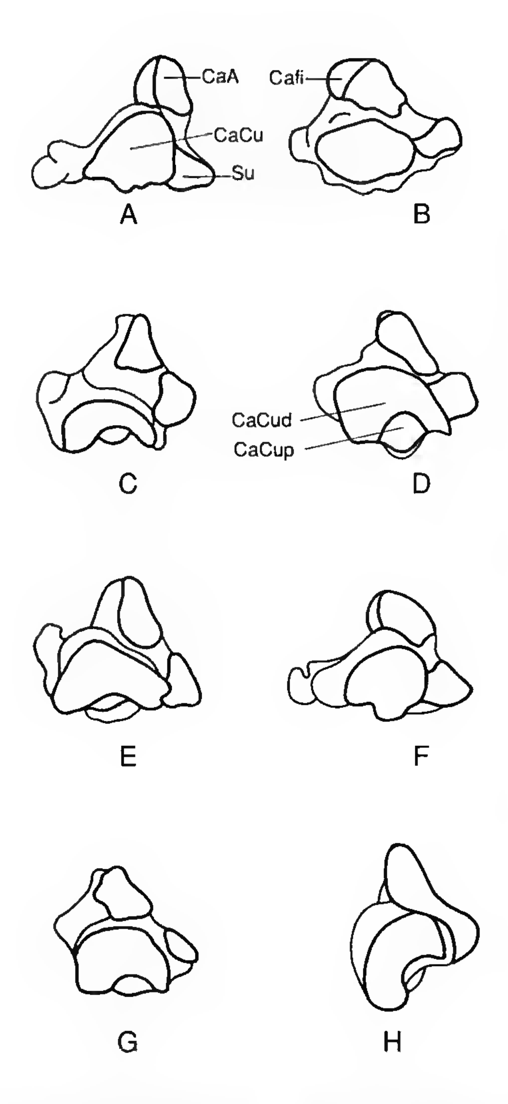


FIG. 56. — Distal view of the right calcaneum of several marsupials: **A**, *Mayulestes*; **B**, *Sipalocyon*; **C**, *Caluromys*; **D**, *Didelphis*; **E**, *Marmosa*; **F**, *Pucadelphys*; **G**, *Metachirus*; **H**, *Phalanger*. Abbreviations: **CaA**, calcaneoastragalar facet; **CaCu**, calcaneo cuboid facet; **CaCud**, dorsal calcaneocuboid facet, **CaCup**, posterior calcaneocuboid facet, **CaFi**, calcaneofibular facet; **Su**, sustentacular facet. Not to scale.

culation must be the most perpendicular as possible to the direction of the force and a dorsal orientation of the ectal facet of the calcaneum reduces the possibilities of medial sliding of astragalus in relation to the calcaneum. In didelphids, the astragalus is not positioned above the calcaneum but on its medial side and the astragalocalcanear facets are oriented medially. As stated above, the articular surfaces must be as close as possible to a position perpendicular to the direction of major forces in order to reduce the possibilities of dislocation of the joint. Therefore, since the upper and lower ankle joints are grossly parallel, an increase of the medial orientation of the astragalocalcanear articulation will place the calcaneum and the foot in an inverted position and the sole will face medially or ventromedially. The inversion of the foot will tend to maintain the articular surface in a position as close as possible to a perpendicular position in relation to the main axis of the tibia (*i.e.* the orientation of the main force exerted on the articulation). Such a position has been shown above to be basic in a didelphid-like arboreal locomotion. This of course does not mean that the most arboreal didelphid cannot walk or even run on the ground, which *Caluromys* can do perfectly well. It only means that these animals are scansorial and poorly adapted to long or/and fast runs. It is likely that *Sipalocyon*, although certainly not as well adapted to running as a thylacine, had better cursorial ability than any didelphid. The morphology of the lower ankle joint of *Mayulestes* with a medially oriented ectal facet, is similar to that observed in the most arboreal didelphids and is therefore compatible with arboreal life. It certainly does not suggest major terrestrial cursorial ability.

Table 11 illustrates the proportions of the tuber calcanei of several marsupials. Among the South American taxa, *Mayulestes* and *Argyrolagus* have a tuber calcanei longer than half of the total length of the bone. A long tuber calcanei is obviously an advantage to increase the power of the extension of the ankle. This movement is useful to run (ungulates, canids) to dig (aardvarks, armadillos, bandicoots) and to jump (kangaroos, bandicoots, *Argyrolagus*, jerboas, gerbils). It has been shown above that numerous features of *Mayulestes* indicate arboreality, but not cursoriality. Therefore, it seems more likely that its long tuber calcanei is related to some leaping ability or a leaping run as in tupaiids but probably less agile. Digging adaptations are improbable.

The tuber calcanei of *Mayulestes* is deep and narrow. As stated by Szalay (1994: 329, fig. 6.16), this morphology indicates strong plantar flexor musculature related to grasping and therefore

TABLE 11. — Comparison of the proportions of the calcaneum in various marsupials. **Lt**, total length; **Ltu**, length of the tuber. All measurements are in millimeters.

	Lt	Ltu	Ltu/Lt
Mayulestes (MHNC 1249)	9.4	5.3	0.55
Sipalocyon (YPM PU 15154)	21	9	0.43
Didelphis	12	5.7	0.47
Pucadelphys (YPFB Pal 6106)	5.9	3	0.5
Caluromys	8.2	3.6	0.43
Metachirus	10.7	5.3	0.5
Perameles	22	15	0.71
Argyrolagus	8.8	5.25	0.59

arboreality. A similar morphology is also found in *Pucadelphys*.

The proximodistally elongated ectal facet of the calcaneum of *Mayulestes* and its sustentacular facet, prolonged both proximally and distally, suggests enhanced capacity of movement between the astragalus and calcaneum (Godinot & Prasad 1994). The morphology of the lower ankle joint therefore suggests good rotational ability of the foot as is observed in several living arboreal mammals.

The large and distal peroneal process of the calcaneum of *Mayulestes* is similar to that of *Deccanolestes hisplopi* (Godinot & Prasad 1994; Prasad & Godinot 1994). According to these authors, this morphology is indicative of the relatively large size of the peronei longus and brevis and adductor digiti quinti, muscles involved in movement of eversion-inversion of the foot. As they mentioned it indicates "[...] frequent foot rotation movements necessary in an arboreal way of life" (Godinot & Prasad 1994: 80).

The sustentaculum tali is weaker in *Mayulestes* and in most living didelphids than in *Sipalocyon*. The large size of the sustentaculum in *Sipalocyon* is probably related to plantigrade terrestrial locomotion. The small size of the sustentaculum of *Mayulestes* indicates that it was much less terrestrial than *Sipalocyon* and is in agreement with the hypothesis of the arboreal habits.

Metatarsus. As shown in table 12 the proportions of the MtIII of *Mayulestes* are slightly inferior to one third of that of the tibia. In *Didelphis*, *Caluromys* and *Marmosa*, the proportion of the MtIII is between one fourth and one fifth the length of the tibia, in *Phalanger* it equals one fifth and in *Philander* it is less than one fifth. In *Megazostrodon*, the relative length of the medial metatarsals can be evaluated to one third of the length of the tibia. In *Henkelotherium* they are less than one third of the length of the tibia and in *Ptilodus* they are slightly longer than the third of the tibia. In *Pucadelphys* the proportion is intermediate between one fourth and one third. Considering the condition of living didelphids, it seems that the shorter MtIII are related to arboreal forms (*Caluromys*, *Didelphis Philander* and *Marmosa*) while the more terrestrial genera (*Metachirus* and *Monodelphis*) have relatively longer MtIII. This idea has been implicitly expressed by Marshall & Sigogneau-Russell (1995). However, highly arboreal squirrels have a MtIII approximating one third of the length of the tibia. *Megazostrodon*, *Henkelotherium* and *Ptilodus* have much longer MtIII than arboreal Recent didelphids and, nevertheless, have been interpreted as arboreal respectively by Jenkins & Parrington (1976), Krause & Jenkins (1983) and Krebs (1991). Furthermore, the MtIII of *Mayulestes* is propottionally longer than that of *Caluromys* or *Didelphis* and it has been shown above that this genus bears several features in its postcranial anatomy which are compatible with

TABLE 12. — Relative length of the MtIII and the tibia in various mammals.**LMtIII**, length of the MtIII; **Lti**, length of the tibia. All measurements are in millimiters.

	LMtIII	Lti	LMtIII/Lti
Mayulestes (MHNC 1249)	13.3	40.5	0.328
Pucadelphys (YPFB Pal 6106)	7.1	24e	0.29
Didelphis	18	83	0.21
Caluromys	8.2	37.6	0.21
Monodelphis	6.6	26.3	0.25
Marmosa	4.4	21	0.21
Phalanger 1	21.5	106	0.21
Metachirus	18	66	0.27
Philander	7.6	41	0.185
Henkelotherium	4	14	0.28
Ptilodus	11.8	28.8	0.41
Megazostrodon	6	18.8	0.32
Sciurus	22.5	66.5	0.3

arboreality. Therefore, relatively long metatarsals appear to be not so closely related to terrestrial habits. They do not seem to be exclusive of arboreal habits but could just represent a plesiomorphic condition.

Conclusions on the postcranial skeleton

The postcranial skeleton of *Mayulestes* has revealed several features that indicate a great similarity with the living didelphids or/and which are compatible with arboreality.

Characters related to arboreality are: (1) the prehensile tail (if actually present in *Mayulestes*); (2) the anterior and distal development of the acromion; (3) the elevation of the spine of the scapula which indicates a powerful musculature necessary to the stability of the scapulohumeral articulation; (4) the great mobility of the scapulohumeral articulation attested by the circular shape of the head, its proximal orientation and the relatively low tubercles; (5) the large size of the epicondyloid ridge and the distomedially protruding medial epicondyle which denote frequency and strength in the movements of the hand and fingers; (6) the great length of the olecranon, strongly bent anteriorly and medially and which is excavated medially by a deep fossa for the flexor muscles of the hand and fingers; (7) the morphology of the McV which denotes good grasping ability; (8) the shallowness of the acetabulum and the excavation of its dorsal border which indicate an important mobility of the coxofemoral articulation; (9) the large size of the trochanters of the femur and the medially bent greater trochanter which also indicate a great mobility of the hip; (10) the sigmoid morphology of the diaphysis of the tibia which indicates the great variety of force directions exerted on the bone; (11) the morphology of the distal articular surface of the tibia which indicates that an extension of the foot was accompanied by inversion; (12) the narrow and proximodistally elongated ectal facet of the calcaneum; (13) the laterally oriented ectal and sustentacular facets (*i.e.* the lower ankle joint) which indicates that the proximodistal resultant forces exerted on the joint will be oriented perpendicular to it (which allows the best stability of the joint and avoids its dislocation) only if the foot is inverted; (14) the proximodistal length of the sustentacular facet which is indicative of good rotational ability of the foot; (15) the large size of the peroneal process which indicates the large size of three muscles involved in movements of eversion-inversion; (16) the elevated and narrow tuber calcanei which indicate strong flexors of the foot and therefore good grasping ability.

Some features are not strictly related to arboreality but are compatible with this way of life and are informative on the locomotion of *Mayulestes* and indicate a relatively agile animal capable of bounding. They are: (1) the posterior position of the anticlinal vertebra (L4) which indicates that *Mayulestes* was not cursorial; (2) the size of the neural spine and transverse processes of the posterior lumbar vertebrae which indicates a powerful epaxial musculature; (3) the morphology and the position of the pre- and postzygapohyses of the last thoracic and lumbar vertebrae which denote an important mobility of the posterior vertebral column; (4) the long, anteriorly bent olecranon of the ulna, which indicates powerful extensions of the elbow (for instance for leaping); (5) the everted iliac wing and the ventrolaterally oriented anteroventral iliac spine which indicates a powerful epaxial musculature, importance of the flexion-extension movements of the column and mobility of the coxofemoral articulation; (6) the relative depth of the femoral trochlea and the elevation of its crests which are related to agility of the animal; (7) the flattening of the proximal epiphysis of the tibia which is also found in some saltatorial lemuriforms; (8) the relative length of the tuber calcanei which indicates leaping and/or running ability.

Furthermore, the elongation and the great dimensions of the neural spine of the axis are indicative of a robust nucchal musculature compatible with predaceous habits.

Habits of Mayulestes ferox

The question of arboreal *vs* terrestrial habits have been discussed by Jenkins & Parrington (1976). The authors stated that the behavioural factor is essential since in arboreal groups some taxa are terrestrial because of any kind of preferences (feeding, physiological, ethological, etc.) even if

they can climb perfectly well. However, Jenkins (1974: 91) stated that "the evidence for locomotory behaviour in both captive and wild tree shrews indicates a moderate diversity of habitat preference. Clearly some tree shrew species are more arboreal than others; other species are more or less terrestrial. Perhaps the most significant fact is that all tree shrews species can climb and, at least occasionally, if not frequently, do so". The same is true for didelphids, where the terrestrial genera *Metachirus* and *Monodelphis* are reported as good climbers (Novak & Paradiso 1983). Hildebrand (1961: 249), who stated (referring to the didelphid genera *Metachirus*, *Monodelphis*, *Philander*, *Didelphis Marmosa*) that "the more arboreal animals differ from the semiarboreal and terrestrial animals in behaviour pattern but not in morphology. Any of them could climb or walk well if it 'wanted' to". Contrary to Hildebrand statement, clear anatomical differences can be related to the arboreal; semiarboreal or terrestrial habits in didelphids. Detailed analysis of the postcranial skeleton reveals morphological differences for almost

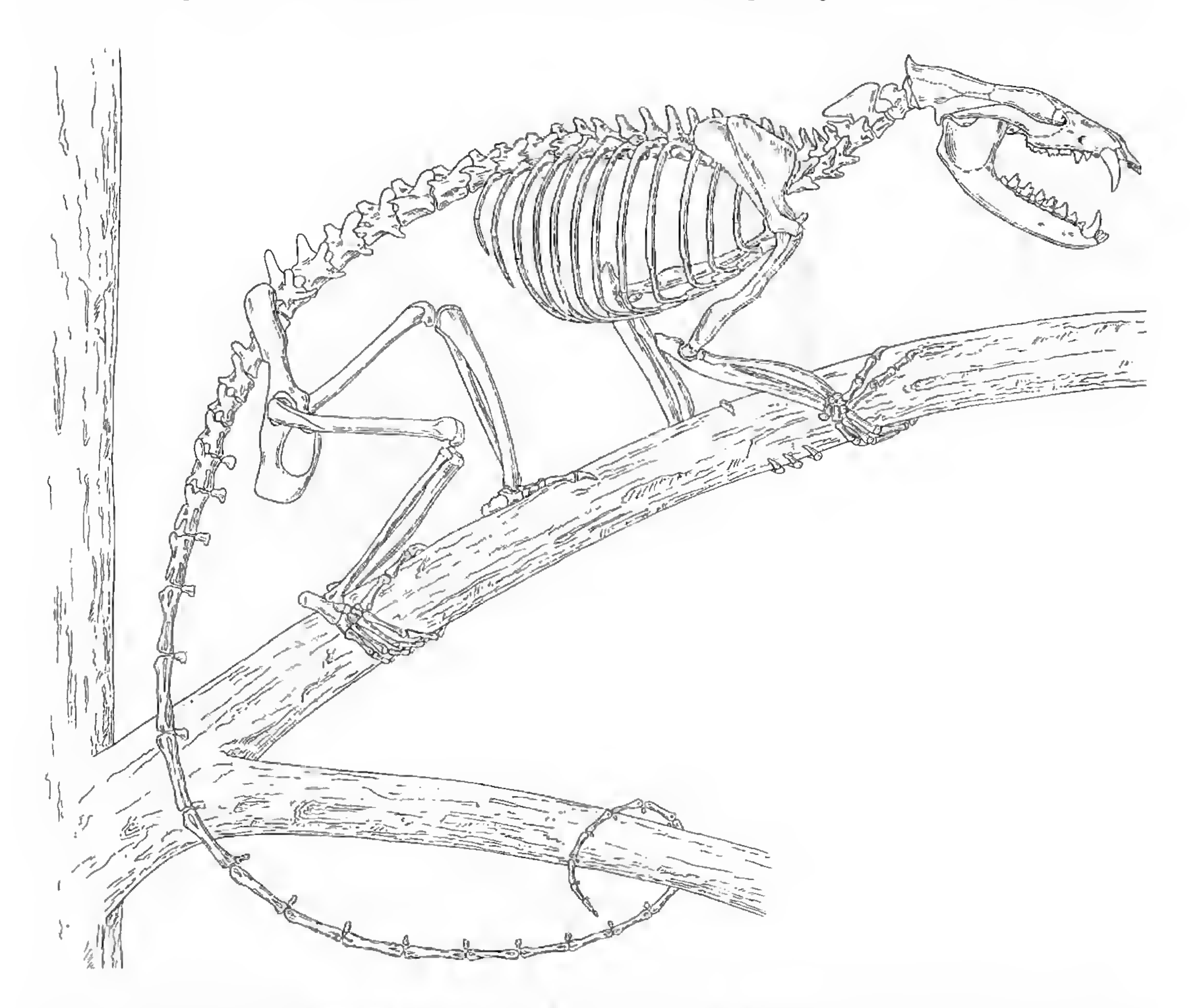


Fig. 57. — Reconstruction of the skeleton of *Mayulestes ferox* (approx. × 0.7). The elements of the skeleton which are missing in the holotype are inspired by the recent arboreal genera *Caluromys* and *Didelphis* rather than the terrestrial Santa Cruz borhyaenoids. In this reconstruction, the tail is regarded as prehensile because of the morphology of C8? and C9? and the number of caudal vertebrae is estimated to approach 30 (as in *Caluromys* where it varies from 30 to 35). The manus and pes are also regarded as prehensile, as in living didelphids and it is hypothesized that *Mayulestes* could have used (at least sometimes) an arboreal way of locomotion similar to that observed in the Recent arboreal didelphids.

every limb bone, some of which can be related to their habits. Furthermore, Grand (1983) has related the difference in limb proportion of *Metachirus* and *Monodelphis* to their way of locomotion. The most important fact is certainly, as stated by Jenkins (1974) for tree shrews, that in both groups (tupaiids and didelphids) all the species can climb well [except perhaps *Metachirus* (Atramentovitz pers. comm.)]. This indicates that for both families arboreality is probably a plesiomorphy. Therefore, since changes in habits is mainly due to behaviour, it is probable that features of the postcranial skeleton of these mammals (whether arboreal, semiarboreal or terrestrial) actually represent arboreal way of life. Since behaviour is not observable in fossils it is obvious that an animal regarded as actually arboreal could be a terrestrial form with a skeleton bearing arboreal features (like *Monodelphis* or *Tupaia tana*). To conclude, another important remark of Jenkins (1974: 91) is that the range of adaptive types is probably too subtle to be understood in terms of the gross categories of arborealism and terrestrialism. It is likely that these two poles are separated by a great amount of intermediate stages representing a gradient from one condition to the other.

In the following interpretation, if a clear position is taken concerning the way of life of *Mayulestes*, it is obvious that behavioural parameters, which could have notably modified the conclusions exposed below, could not be taken into account. Given the preceding discussions and lists of characters, it is highly probable that *Mayulestes* was at least partially arboreal. Its mode of locomotion could have approached that of tupaiids (although certainly not as fast and agile) weasles, or *Metachirus* (on the ground). The postcranial skeleton of *Mayulestes* shows ability for leaping or bounding, which is in agreement with predaceous habits. It is likely that *Mayulestes* was more agile than most living didelphids. *Mayulestes* was certainly not exclusively arboreal as is *Caluromys* and it probably spent part of its time on the ground, perhaps under the pressure of some alimentary or ethological factors. With its short limbs and its short and blunt snout (when compared to didelphids), *Mayulestes* probably had an external aspect similar to that of the living weasels (Fig. 57). Although it was certainly more arboreal (most of the weasels climb well but are not considered arboreal mammals), its agility was probably similar. Like weasels, *Mayulestes* was certainly an efficient predator which could have fed upon the abundant fauna of small insectivorous marsupials (*Pucadelphys*, *Mizquedelphys*, *Incadelphys*, *Tiulordia*, *Peradectes*, *Kahsia*, *Jaskhadelphys*). In size, these animals are similar to the small rodents that make an important part of the diet of the various species of *Mustela*. Weasels are known (Novak & Paradiso 1983) to attack sometimes animals much larger than themselves (*i.e.* adult hares). A further comparison of *Mayulestes* with *Mustela* therefore suggests that larger omnivorous animals like the small condylarths of Tiupampa (*Tiuclaenus*, *Molinodus* or *Pucanodus*) or caroloameghiniids such as *Roberthoffstetteria* could have also represented occasional prey for *Mayulestes*. Larger didelphids such as *Andinodelphys*, other predaceous marsupials like *Allqokirus* and the large (for the fauna) pantodont *Alcidedorbignya* are less probable to have represented easy prey for *Mayulestes*. Among the non-mammalian fauna, the leptodactylid frog *Estesius* is very likely to have represented an important part of the diet of *Mayulestes*.

Evolution of the locomotion and habitat preferences of the borhyaenoids

The other borhyaenoids known by partial skeleton are the four genera of the middle Miocene Santa Cruz beds of Patagonia: *Cladosictis*, *Sipalocyon*, *Prothylacynus* and *Borhyaena* and the skeleton of *Lycopsis* from the late Miocene of La Venta (Colombia; Marshall 1977a). They are much larger animals than *Mayulestes* and range in size from a small fox to a small bear. They were terrestrial and show some cursorial adaptations, although they are not as highly adapted as thylacines or canids. Several features of their postcranial skeleton indicate an intermediate morphology between *Mayulestes* and thylacines. They are: (1) the anterior position of the anticlinal vertebra (on the last thoracics); (2) the straightness of the ulna, whose olecranon is long but not bent anteriorly (in *Borhyaena* the diaphysis of the ulna is even bent posteriorly as in

all cursorial mammals); (3) the straightness of the femur, whose proximal epiphysis is not bent medially; (4) the straightness of the tibia; (5) the strong development of the tibial tuberosity; (6) the anteroposterior orientation of the medial malleolus of the tibia, which restricts the ankle movement to flexion-extension; (7) the reduction of the hallux.

However, some features clearly indicate that the Santa Cruz borhyenoids were not highly cursorial mammals. They are: (1) the development of the epicondyloid crest and medial epicondyle of the humerus, indicating a good mobility of the hand and fingers, which is generally not found in cursorial mammals; (2) the absence of a posterior curvature of the femur, a feature present in thylacines and canids; (3) the weak (when compared to cursorial mammals) excavation of the femoral trochlea, which denotes slower and weaker movements of the knee (in other words, less stress in the femorotibial articulation); (4) the semiplantigrady attested by the morphology of the tarsus.

Among the Santa Cruz borhyaenoids, however, some differences can be noted in the anatomy of the limbs bones and, therefore, in morphofunctional interpretation. In *Prothylacynus*, the humerus has a relatively circular head as in *Mayulestes*, which indicates a greater mobility of the shoulder than in *Cladosictis*, where the humeral head is clearly elongated anteroposteriorly (Table 3) and matches the W/L ratio observed in *Metachirus* and *Thylacinus*, respectively, cursosaltatorial and cursorial marsupials (the humerus of *Borhyaena* is unknown). Nevertheless, because of the higher greater tuberosity of its humerus, the shoulder of *Prothylacynus* must have been less mobile than that of *Mayulestes*. In *Prothylacynus* the presence of a deep fossa on the posterior face of the lesser tuberosity and medial border of the head indicates a powerful accessory head of the triceps. This condition denotes important capacities of extension or retention to flexion of the elbow. The extremely developed entepicondylar crest of the humerus is related to good mobility of the manus (pronation-supination and flexion-extension). The capitulum of the humerus and the humeral articulation of the radius are oval-shaped (only slightly wider than long) which indicates a fairly good capacity for pronation-supination movements. The radius of *Prothylacynus* bears along its shaft (as in *Caluromys*) a well-developed lateral crest which receives part of the origins of the pronator quadratus (on the posterior side) and abductor pollicis longus (on the anterior side). These muscles are generally attached on the interosseous membrane and the presence of a well-developed medial crest of the radius, which partially fills the interosseous space indicates much stronger muscles. The medial face of the olecranon of the ulna bears a deep medial fossa for the flexor of the manus and fingers. Therefore, the morphology of the elbow and forearm of *Prothylacynus* indicates an enhanced mobility of the elbow, wrist and fingers.

In *Borhyaena*, the humerus is unknown, but the ulna is highly informative. The shaft of the bone is slightly recurved posteriorly and the apex of the olecranon extends posterodistally, whereas, in *Prothylacynus* the ulna is globally straight but slightly convex posteriorly, at the level of the radiohumeral articulation. In *Cladosictis* the ulna is intermediate between those of *Borhyaena* and *Prothylacynus*. Contrary to the condition observed in *Prothylacynus*, the flexor fossa of *Borhyaena*, on the medial face of the olecranon, is shallow as in thylacinids and canids. The beak of the olecranon protrudes anteriorly to a greater extent than in *Prothyalcinus* and the greater sigmoid cavity is less open than in *Prothylacynus*. This condition of the elbow articulation of *Borhyaena* indicates a greater stability of the joint than in *Prothylacynus* in order to tolerate a greater stress (for instance when running). The humeral articulation of the radius in *Borhyaena* (W/L ratio = 0.59) and *Cladosictis* (W/L ratio = 0.606) is much more transverse than in *Prothylacynus* (W/L ratio = 0.77) and the lateral border of the shaft is rounded and bears no crest as is observed in *Prothylacynus* and *Caluromys*. This morphology is indicative of lesser mobility of the forearm, manus and fingers than in *Prothylacynus* and is in agreement with better cursorial abilities. The condition of the humerus head of *Cladosictis* (much longer than wide) denotes a predominance of parasagittal movements of the forelimb. It is therefore possible that *Borhyaena* and *Cladosictis* were, at least par-

tially, cursorial or semicursorial. *Prothylacynus* has a forelimb compatible with agility and good capacity of grasping (possibly some climbing). However, the protruding tibial tuberosity of *Prothylacynus* also indicates a great power of the knee extensors compatible with some running (or/and bounding) ability (the tibia of *Borhyaena* is unknown and that of *Cladosictis* also has a strong tibial tuberosity). The locomotory habits and other limb uses of *Prothylacynus* could grossly approach those of living bears or large felids which have fairly mobile forelimbs (although very probably less than *Prothylacynus*) and which are capable of very fast running (especially felids). *Prothylacynus* could have had a forelimb slightly more agile than that of living bears (with reasonably good climbing ability as bears) and could have been a slightly better runner than bears (bears have an anteroposteriorly shorter proximal epiphysis of the tibia) but certainly not as fast as a felid. It is very probable that *Borhyaena* was a better runner and had lesser mobility of the forearm than *Prothylacynus*. *Borhyaena* and *Cladosictis*, seem to have initiated a cursorial adaptive trend whose extreme specialisation is observed (among marsupials) in the thylacine. *Prothylacynus* and *Borhyaena* are similar in size and coexisted in the same environment of the Santa Cruz beds; they should therefore have had different ecological niches. As a matter of fact, the morphology of their limb bones certainly indicates different habits, although the determination of their mode of locomotion and other use of the forelimbs still remains poorly defined.

The Santa Cruz borhyaenoids were efficient predators, although to various degrees (Sinclair 1906). Some features indicate that they were more predators than scavengers. They are: (1) the very large and elongated morphology of the neural spine of the axis which denotes the strength of the neck musculature necessary when seizing a prey; (2) the eversion of the iliac wings which indicates a powerful epaxial musculature necessary for leaping onto prey; (3) the presence of large claws; (4) the presence of some running ability as indicated by the morphology of the knee.

Therefore, the large and medium-sized Miocene borhyaenoids were terrestrial animals (with perhaps some arboreality in *Prothylacynus*) capable of relatively efficient running (to a greater extent in *Borhyaena*) but probably for a short distance. Since they were predators, in order to seize prey such as the relatively fast-running notoungulates and litopterns, it is likely that they had to hunt lying in wait as ambush predators, bounding on their prey at the appropriate moment in a way somewhat comparable to that of the living felids (this is especially true for *Prothylacynus*). Because of their relatively short limbs (Sinclair 1906) and the fact that they were semiplantigrade, it is probable that they were not capable of such a fast running as the living felids and, hence, were probably not as efficient.

Mayulestes, the oldest known borhyaenoid, was partially arboreal and its mode of locomotion was probably a moderately fast weasel- or tupaiid-like leaping run. Geologically younger borhyaenoids from the Miocene are terrestrial and probably scansorial with good ability for bounding. *Borhyaena* and *Cladosictis* were probably better runners than *Prothylacynus*, which could have had some climbing ability.

Way of life of Pucadelphys

Marshall & Sigogneau-Russell (1995) have suggested a terrestrial mode of life for *Pucadelphys*, a didelphoid from Tiupampa. However, this study has pointed out several features of *Pucadelphys* which indicate that it was, at least partially, arboreal. The features mentioned above are: (1) prehensile tail (*contra* Marshall & Sigogneau-Russell 1995); (2) large acromion developed anteriorly and distally; (3) humeral head approximately as wide as long with relatively low tubercle denoting a good mobility of the shoulder; (4) very large epicondyloid crest and medial epicondyle which indicate important capacity for flexion and extension of the hand; (5) olecranon of the ulna strongly bent anteriorly; (6) olecranon bent medially, with a deep medial fossa for the flexors of the manus and digit; (7) salient crest of the pronator quadratus on the medial side of the distal extremity of the diaphysis of the ulna; (8) acetabulum relatively open with an excavated dorsal border (concave laterally), which indicate a good mobility of the coxofemoral articulation; (9) strong development of the femoral trochan-

ters which also indicates good mobility of the hip; (10) helical astragalar facet on the tibia, which allows inversion movements of the foot; (11) large peroneal process of the calcaneum which also indicates frequent inversion-eversion movements of the foot; (12) elevated and narrow tuber calcanei which denotes strength of the digital flexors of the pes; (13) sustentacular facet medially oriented and distally extended; (14) capacity of hind foot reversal as indicated in Marshall & Sigogneau-Russell (1995, figs 25A, 41, 45 and 48) and as corroborated by the morphology of the astragalar trochlea observable after further preparation of specimen YPFB Pal 6106.

Considering the morphology of its lumbar vertebrae and ilium, *Pucadelphys* was probably fairly agile and was probably capable of leaping, as stated by Marshall & Sigogneau-Russell (1995). Digging ability suggested by these authors is possible although *Pucadelphys* does not show any undoubted and exclusively fossorial adaptation such as finger modifications (stoutness of the metapodials, large claws). In fact, many non-fossorial mammals can dig (some dasyurids, many canids, lagomorphs, many non-hyperfossorial rodents, some viverrids, tenrecids, solenodontids, some soricids, some macroscelids). However, the association of arboreal adaptations to the lack of obvious fossorial adaptations seriously reduces the credibility of true fossorial habits in *Pucadelphys*. The specialisations of the pelvis of *Pucadelphys* mentioned by Marshall & Sigogneau-Russell (1995: 149, 150) are also, as the authors mention, leaping adaptations. Furthermore, the authors compare *Pucadelphys* with *Perameles* which they consider as a digging form. If it is true that *Perameles* often forages the ground in search for food, it is also an extremely agile runner and leaper which is also responsible for the morphology of its ilium. This well-known adaptation of *Perameles* (Novak & Paradiso 1983) is never mentioned by Marshall & Sigogneau-Russell (1995). Given the discussion above, it seems more probable that locomotion in *Pucadelphys* was a sort of leaping run similar to that of *Metachirus*, although probably not so agile. Cifelli *et al.* (1988) have shown that, in primitive tribosphenid mammals, "terrestrial species are clearly distinguished from arboreal form on the basis of their more heavily pitted and deeply striated crushing and shearing surfaces respectively on molar crowns". These microwears, in terrestrial forms is probably due to the dust, sand grains and earth which is ingested with aliments on the ground. It is likely that this condition should be greatly enhanced in the case of a fossorial species. However, since *Pucadelphys* was probably both arboreal and terrestrial it is probable that the observation of well-marked microwear features would not be of great significance. Considering the influence of ethological factors in arboreality *vs* terrestriality, it is not possible to determine if *Pucadelphys* was more or less terrestrial than arboreal. It is clear, however, that it had arboreal ability. It may have represented a stage close to the plesiomorphic condition.

Arboreality vs *terrestriality*

The interpretations presented here of the way of life of *Mayulestes* and *Pucadelphys* require the combined presence of a prehensile tail and a relative agility with reasonable running and leaping ability. However, as mentioned by Cartmill (1974: 51), no living animal with a prehensile tail has an extremely agile arboreal locomotion except the acrobatic ceboids. Nevertheless, the combination of a prehensile tail with agile leaping and running is well known in *Metachirus*, a terrestrial didelphid. In this case, the prehensile tail of *Metachirus* is not used for climbing but probably represents a plesiomorphic feature, heritage of the arboreal ancestor of *Metachirus*. Therefore, a plausible interpretation could be that *Mayulestes* and *Pucadelphys* were both arboreal and terrestrial (which is highly probable) and that their agility was mainly used on the ground. Their arboreal locomotion was probably more cautious which would be in agreement with Cartmill's statement. Two other interpretations in agreement with Cartmill's statement could be considered: (1) *Mayulestes* was terrestrial but recently evolved from an arboreal ancestor, thus retaining several arboreal features on its skeleton; the agility of *Mayulestes* would therefore be derived as is that of *Metachirus*; (2) *Mayulestes* was mainly arboreal but is derived in

having acquired agility and lost a great part of the prehensility of its tail; *Mayulestes* would have had an arboreal locomotion close to that of squirrels or tree shrews. This interpretation implies that the plesiomorphic condition is a relatively slow locomotion with a prehensile tail (didelphid-like) which is far from being demonstrated. In other respect, it is noteworthy that arboreal conditions in the early Palaeocene do not have to be similar to those in the present. The fact that some features of *Mayulestes* and *Pucadelphys* indicate agility combined with a prehensile tail is perhaps an evidence which contradicts Cartmil's statement. In fact, it is probable that the actual locomotor biology of *Mayulestes* was more eclectic than the four hypotheses proposed above. The arboreal features of *Mayulestes* indicate that it was very probably capable of climbing, it probably had a prehensile tail, it was probably partially terrestrial and it was relatively agile. How these four characteristics combine and their relative importance in the biology of *Mayulestes* is difficult, perhaps impossible, to establish so far. It seems reasonable to conclude that *Mayulestes* had good potential for arboreality, agility and prehensility of the tail; *Mayulestes* is not an extremely derived arboreal mammal and certainly was also partially terrestrial.

Therefore, analysis of the postcranial skeleton of *Mayulestes* shows that the evolution of borhyaenoids is characterized by a loss of arboreality. This would indicate that this adaptation is a marsupial symplesiomorphy within the superfamily. Furthermore, the almost universal arboreality (or climbing ability) of the didelphoids (including *Pucadelphys*) also indicates that arboreality probably represents the plesiomorphic way of life of this group. The morphofunctional study of the Tiupampa marsupial skeletons therefore seems to corroborate the conclusions of Szalay (1984: 254) that the stem marsupials were primarily arboreal mammals.

GENERAL CONCLUSIONS

Mayulestes ferox is the oldest known borhyaenoid represented by a skeleton and is the most primitive member of the superfamily. It is represented by one of the two oldest known skeletons of American marsupials. Dental morphology clearly indicates an animal engaged in the way of hypercarnivorous specialisation, although relatively discretely. The development of a prevallid-postvallum shear (and the related transformations of the tooth morphology) is a common adaptation among meat-eating mammals and has appeared at least in six different groups of mammals and very probably several times within each group. It is therefore a highly homoplastic apomorphy which has reduced phylogenetic value. One apomorphy of *Mayulestes* also found in the contemporaneous genus *Allqokirus* is the reduction of the entoconid, which is regarded here a synapomorphy of the family Mayulestidae. Because of the presence of a reduced entoconid, the Mayulestidae cannot be ancestral to the late Palaeocene genus *Patene* from Itaboraí which has a well-developed entoconid. On the other hand, they constitute a good potential dental ancestor for cf. *Nemolestes* sp. from the same locality, a primitive Borhyaenidae which has lost its entoconid and has a reduced metaconid. However, cranial remains from this genus are needed to test this hypothesis.

The presence, in *Mayulestes*, of five upper and four lower incisors (I4/i3, in other borhyaenoids) reinforces the fact that I5/i4 is the primitive marsupial incisor formula.

The skull of *Mayulestes* is highly informative on marsupial basicranial structure. Comparison with the other oldest-known marsupial skeleton, *Pucadelphys andinus*, reveals that the tympanic process of the alisphenoid and the alisphenoid hypotympanic sinuses, characteristic of marsupials, are very likely to have appeared several times within marsupial evolution. Therefore, they should not be considered as diagnostic synapomorphies of the Metatheria. In all bothyaenoids the squamosal participates in the formation of the alisphenoid sinus. This character state, which is absent from all the other marsupials represents one of the main synapomorphies of the superfamily. Most of the other cranial features of *Mayulestes* are therian, tribosphenidan, or marsupial plesiomorphies.

The postcranial skeleton of *Mayulestes* clearly indicates an animal that was at least partially

arboreal. Many features are shared with the didelphoids (including *Pucadelphys*) which are primirively arboreal (secondarily terrestrial for some forms). *Pucadelphys* is regarded here as partially arboreal contrary to former interpretations (Marshall & Sigogneau-Russell 1995). Among the many arboreal features borne by *Mayulestes* some are shared with other arboreal therian and non-therian mammals. A medial distal condyle of the femur that is narrower than the lateral condyle is found in *Mayulestes*, *Pucadelphys*, the living didelphids, phalangerids, *Dendrolagus*, *Eozostrodon*, *Megazostrodon*, *Erythrotherium*, arboreal multituberculates (*Stygimys*, *Ptilodus*, ? *Eucosmodon*, ? *Mesodma*) and *Henkelotherium*. A sigmoid tibia is found in *Mayulestes*, in all living didelphids, in phalangerids (less marked than in didelphids), in *Eozostrodon*, in arboreal multituberculates (*Ptilodus*, ? *Mesodma*) and in *Henkelotherium*. Considering their distribution these two features are probably plesiomorphic. However, it is noteworthy that they are present only in living arboreal marsupials (although not in all of them) or in fossil mammals interpreted as arboreal. They are absent in the Asian multituberculates, regarded as terrestrial by Kielan-Jaworowska & Gambatian (1994). Therefore, these features are very probably related to some kind of arboreality. If these hypotheses are correct, they would indicate that some arboreal features are plesiomorphic for mammals. This does not imply that arboreality is a plesiomorphic feature for mammals as hypothesized by Matthew (1904). Furthermore, as clearly stated by Jenkins & Parrington (1976) arboreality is a very relative state since the influence of behaviour may greatly influence the habits of mammals. Moreover, as stated by Jenkins & Parrington (1976: 425, 426) the question of arboreal *vs* terrestrial specialisation in diminutive mammals is probably invalid since at "ground level, obstacles that requires climbing are common and vegetation provides a continuum of substrate possibilities between the terrestrial and the arboreal". It is also noteworthy that several Late Cretaceous mammals from Mongolia (eutherians and multituberculates) have been regarded as terrestrial (Kielan-Jaworowska 1977, 1978; Kielan-Jaworowska & Gambaryan 1994); undoubtedly this is related to the very arid environment in which they were living. Although the study of the postcranial morphology of *Mayulestes* and *Pucadelphys* does not confirm Matthews (1904) theory, it does not contradict it and certainly reinforces the hypothesis of the ancestral arboreality of marsupials.

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APPENDIX

Following are the measurements of *Mayulestes ferox* in millimeters. e, estimated; –, measurement not available.

Anteroposterior length from the tip of the right premaxilla to the tip of the right condyle	53.4
Anteroposterior length from the tip of the left premaxilla to the tip of the left condyle	52.5
Bizygomatic width	33.5
Width between the lacrimal foramina at the anterior extremity of the orbits	17.8
Width of the rostrum at the anterior opening of the infraorbital canal	13.7
Width of the rostrum between the supraorbital humps (supraorbital processes)	12.8
Minimum width of the interorbital bridge	11
Length of the right temporal fossa	11.6
Length of the left temporal fossa	11.4
Maximum width of the nasals	12.7
Width of the basicranium between the external auditory meati	20.2
Length of the right tooth row (P1-M4)	16.5
Length of the left tooth row (P1-M4)	16.6
Length of the palate in sagittal plane	26.5
Length of the lower cheek tooth row (p3-m4)	20
Internal height of the dentary below middle of M3	7.3

Measurements of the skull: since the crushing of the skull is essentially dorsoventral, the actual horizontal distortion is probably not very important. Therefore, the following measurements represent a reasonable approximation of the actual dimensions of the skull.

Height of the dentary below talonid of m1	7.3
Height of the dentary below talonid of m2	7.1
Height of the dentary below talonid of m3	6.8
Height of the dentary below posterior talonid of m4	6.27
Length of the symphysis	9.15

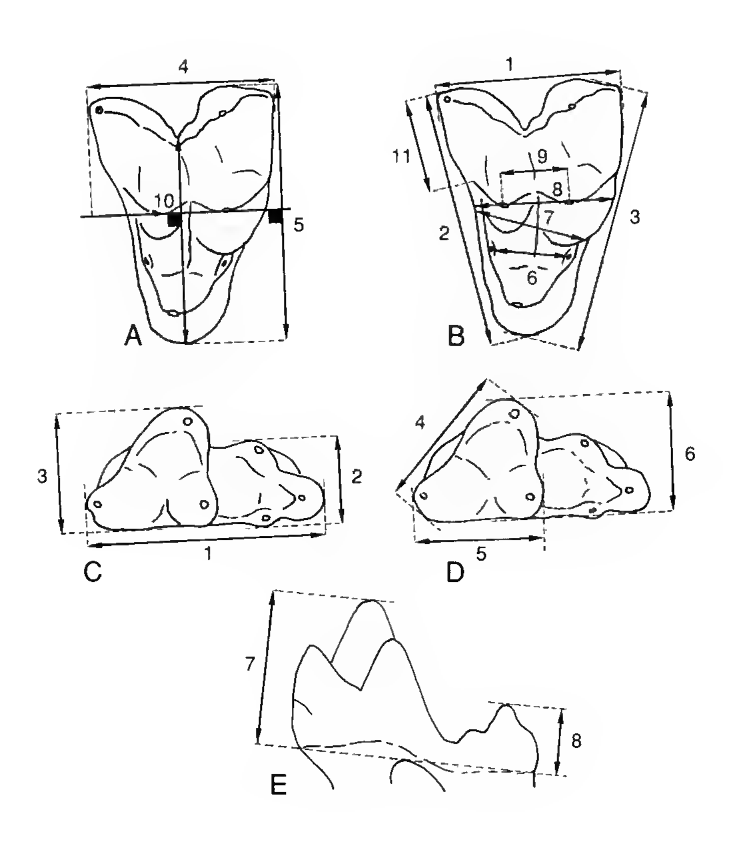
Measurements of the dentary.

	I1		I2		I3		I4		I5	
	L	W	L	W	L	W	L	W	L	W
Upper Right	0.6	0.6	0.5	0.5	–	–	–	–	–	–
Upper Left	–	–	–	–	0.7	0.7	0.7	0.5	0.6	0.4
Lower Right	0.2	0.4	0.3	0.4	0.3	0.3	0.2	0.2		

Measurements of the incisors.

	P1r	P2r	P3 l	p1r	p3 l
L	1.12	2.2	2.6	1.3	2.2
W	0.78	1	1.4	0.6	1.2
H	0.87	1.5	2.5	0.9	2.6

Measurements of the premolars.



	M1r	M2r	M3r	M4r	m1r	m2r	m3r	m4l
1	2.95	3.12	2.96	2.39	2.86	3.06	3.36	3.72
2	3.66	4.08	4.55	1.83	1.11	1.21	1.43	1.2
3	2.48	3.27	3.72	3.68	1,24	1.84	1.87	1.98
4	2.86	3.09	2.89	1.95	1.74	2.2	2.09	2.34
5	3.29	391e	4.29	3.39	1.89	1.91	1.87	2.03
6	1.31	1.42	1.41	0.83	1.19	1.92	1.9	2.07
7	1.46	1.48	1.48	1.02	–	–	3.32	3.54
8	2.1	1.98	1.85	1.27	–	–	1.61	1.48
9	0.99	1.08	1.19	–	–	–	1.6	2.03
10	2.72	3.55	3.5	–	–	–	1.78	1.96
11	1.44	1.47	1.73	–	0.91	0.89	1.34	1.08

Measurements of the molars: upper (**A**, **B**) and lower (**C**-**E**) teeth of *Mayulestes ferox* showing orientations for measurements; **1**-**11**, upper molar, **1**-**8**, lower molar. Unarrowed thick line on A is an axis of orientation.

Maximum length of the neural arch	5.5
Maximum width of the neural canal	6
Maximum width between the lateral borders of the occipital facets	12.5
Maximum width of the intercentrum	6
Maximum height of the left occipital facet	4.2
Maximum width of the left occipital facet	3
Maximum height of the left axoidian face	4.3
Maximum width of the left axoidian facet	3

Measurements of the atlas (CV1).

Maximum length of the neural spine	13
Maximum ventral length	9.5
Maximum height of the axis at the level of the posteroventral border of the centrum	11
Maximum width between lateral borders of the atloidian facets	8.2
Posterior width of the centrum	4.7
Posterior height of the centrum	3
Width between the postzygapophyses	7
Ventral length of the dens	2.9
Height of the dens	1. 5
Width of the dens	2

Measurements of the axis (CV2).

	CV?3	CV?5
Length of the centrum	4	3.7
Anterior width of the centrum	–	4.5
Posterior width of the centrum	4.6	4.3
Anterior height of the centrum	–	2
Posterior height of the centrum	2	2
Width between prezygapophyses	–	9

Measurements of CV?3 and CV?5.

	T?1	T?12	T?13
Length of the centrum	4.2	6.2	6.4
Anterior width of the centrum	4.5	4.6	4.8
Anterior height of the centrum	2.7	2.3	3
Posterior width of the centrum	4.2	4.7	8
Posterior height of the centrum	2.4	2.5	–
Width between transverse processes	11e	–	–
Width between anapophyses	–	7.1	6.7
Width between prezygapophyses	7.3	5.7	–
Width between postzygapophyses	6	4.1	–
Height at level of the spine	–	7.2	7.2
Length of the spine at apex	–	3	2.9

Measurements of thoracic vertebrae.

	L1	L2	L3	L4	L5
Length of the centrum	7	7.4	8.2	9	7.4
Anterior width of the centrum	5.7	4.8	5.2	5.2	5.4
Anterior height of the centrum	–	3.4	2.8	–	3.7
Posterior width of the centrum	4.3	4.8	5.7	5.5	6
Posterior height of the centrum	3	3.2	2.8	3.2	3.7
Width between transverse processes	6.6e	–	–	–	13.7
Length between anapophyses	–	7e	–	–	–
Width between prezygapophyses	6.7	7.5	–	–	9
Width between postzygapophyses	5.7	5.9	5.9	–	7.8
Height of vertebra at level of spine	9	10	–	–	13.5
Length of the spine at apex	3.4	3	2	–	2.3

Measurements of lumbar vertebrae.

	C?1	C?3	C?8	C?9
Length of the centrum	5	6.7	16	16
Anterior width of the centrum	4.3	3.5	5.4	4.8
Anterior height of the centrum	3.5	3.5	3	3.3
Posterior width of the centrum	5	3.5	5.4	5
Posterior height of the centrum	3.3	3.6	3.7	3
Width between anterior transverse processes	–	–	7.5	7.5
Width between posterior transverse processes	–	–	7.3	7
Width between prezygapophyses	6	6	4.8	4
Width between postzygapophyses	–	3e	2.5	2.6

Measurement of the caudal vertebrae.

Maximum length of the infraspinatus fossa, parallel to the spine	25.08
Maximum anteroposterior length parallel to the spine	16.97
Length of the glenoid cavity	5.63
Width of the glenoid cavity	3.77
Maximum anteroposterior length of the acromion	6.14
Proximodistal length of the acromion	9.65
Maximum height of the spine	4.00

Measurements of the scapula

Length	32.54
Transverse width of the head	4.78
Anteroposterior length of the head	4.89
Length of deltoid crest	17.9
Transverse width of proximal extremity	9.91
Maximum width of the distal articular surface in anterior view	6.48
Width of the capitulum in anterior view	3.36
Height of the capitulum in anterior view	1.97
Width of the trochlea in anterior view	1.66e
Height of the trochlea in anterior view	1.75
Height of the capitulum in distal view	3.21
Height of the trochlea in distal view	2.66
Depth of the trochlea in posterior view	0.89
Angle between anterior and posterior edge of trochlea in distal view	56°

Measurements of the left humerus.

Length	37.74
Length from apex of olecranon to coronoid apophysis	10.5
Length of olecranon from apex to proximal extremity of greater sigmoid cavity in medial view	4.72
Maximum anterior length of the olecranon	12
Proximodistal length of greater sigmoid cavity in medial view	6.2
Width of proximal edge of the sigmoid cavity	3.53
Width of olecranon at apex	3.1
Width at the level of the coronoid apophysis	4.68
Anteroposterior length at proximal edge of sigmoid cavity	3.7
Length of medial branch of proximal edge of greater sigmoid cavity	2.58
Length of lateral branch of proximal edge of greater sigmoid cavity	1.48
Angle between olecranon and shaft in anterior view	149°
Angle between olecranon and shaft in lateral view	166°

Measurements of the ulna.

Length	29.46
Width of proximal epiphysis	3.96
Length of proximal epiphysis	–
Length between proximal end and distal border of bicipital tuberosity	5.02
Width of distal epiphysis	4.35
Length of distal epiphysis	2.74

Measurements of radius.

Length	7
Width of diaphysis at mid-length	0.9
Anteroposterior length of diaphysis at mid-length	1.8
Width of distal epiphysis	2.6
Anteroposterior length of distal epiphysis	1.4

Measurements of the metacarpals (McV).

Length	42.57
Length of the ilium from anterior extremity to centre of acetabulum	25.2
Dorsoventral breadth of iliac wing	7.17
Anteroposterior diameter of acetabulum	6.6
Maximum dorsoventral diameter of acetabulum	6.1
Length from posterior border of sciatic spine to posterior border of ischium	11.95

Measurements of the innominate.

Length	40.77
Proximal transverse width	10.23
Length from tip of greater trochanter to ventral border of head	4.13
Length from tip of greater trochanter to distal end of lesser trochanter	10.36
Mediolateral length of the head in posterior view	6.08
Anteroposterior length of the head in proximal view	3.84
Length from tip of greater trochanter to distal end of trochanteric fossa	5.48
Transverse diameter at mid-length of the shaft	3.66
Anteroposterior diameter at mid-length of the shaft	2.76
Transverse width of distal extremity	7.54
Anteroposterior length of lateral distal condyle	6.06
Width of left lateral distal condyle in posterior view	4.2
Width of right lateral distal condyle in posterior view	3.6
Width of right medial distal condyle in posterior view	2.7
Height of right lateral condyle in posterior view	2.35
Width of left trochlear groove	4.2
Width of right trochlear groove	3.5
Lateral height of trochlear groove in anterior view	4.4
Medial height of trochlear groove in anterior view	3.56
Lateral length of trochlear groove in distal view	3.77
Medial length of trochlear groove in distal view	3.11

Measurements of the femur.

Length	40.68
Proximal transverse width	7.5
Proximal anteroposterior length	5.2
Width of the lateral proximal condyle	3.18
Width of the medial proximal condyle	2.59
Anteroposterior length of the lateral proximal condyle	3.17
Anteroposterior length of the medial proximal condyle	3.55
Distal transverse width	4.1
Distal anteroposterior length	3.78
Proximodistal length of malleolus	1.84
Width of the malleolus	2.18
Width of astragalar facet from base of malleolus to lateral edge	1.95
Angle between the flexion axis of the knee (*ca.* greatest width of the proximal epiphysis) and the plane of the malleolus	48°

Measurements of the tibia.

Distal transverse width	4.5
Distal anteroposterior length	3.8

Measurements of the fibula.

Length	9.5
Width of the tuber at mid-length	1.8
Height of the tuber at mid-length	3.2
Proximodistal length of ectal facet	3.3
Transverse width of ectal facet	1.8
Maximum distal width	5.5
Width of cuboid facet	3.3
Dorsoplantar length of cuboid facet	2.7

Measurements of the calcaneum.

	Mt?III	MtIV
Length	13.4	12.1
Proximal width	2.2	2
Distal width	2.8	2.7

Measurements of metatarsals.

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Diffusion Delphine Henry
57, rue Cuvier, 75005 Paris,
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Tél. : 33 - 01 40 79 37 00
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